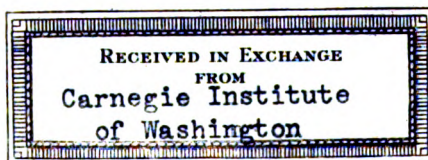
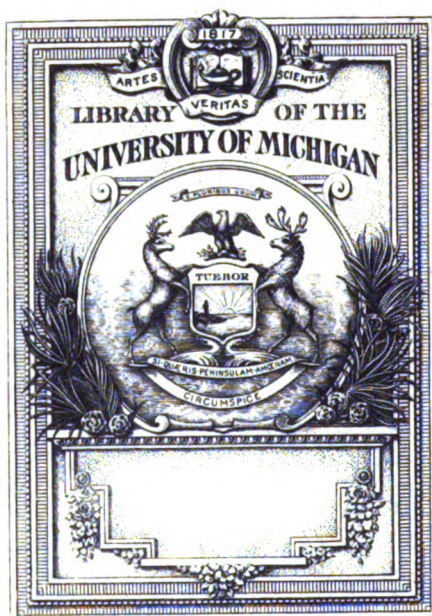


CONTRIBUTIONS TO PALAEONTOLOGY

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MIOCENE AND PLIOCENE
FLORAS OF WESTERN
NORTH AMERICA
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CHANEY, ELIAS, DORF
ALEXROD AND CONDIT



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CONTRIBUTIONS TO PALÆONTOLOGY

MIOCENE AND PLIOCENE
FLORAS OF WESTERN
NORTH AMERICA



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- I. CHANEY, RALPH W. and MAXIM K. ELIAS. Late Tertiary Floras from the High Plains. With a chapter on the Lower Pliocene Vertebrate Fossils from the Ogallala Formation (Lavern Zone) of Beaver County, Oklahoma. By Curtis J. Hesse. Pages 1 to 72, 7 plates and 11 text-figures. (Issued October 1936)
- II. DORF, ERLING. A Late Tertiary Flora from Southwestern Idaho. Pages 73 to 124, 3 plates and 2 text-figures. (Issued November 1936)
- III. AXELROD, DANIEL I. A Pliocene Flora from the Mount Eden Beds, Southern California. Pages 125 to 183, 6 plates and 1 text-figure. (Issued May 1937)
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- V. CONdit, CARLTON. The San Pablo Flora of West Central California. Pages 217 to 268, 7 plates and 1 text-figure. (Issued April 1938)

CONTRIBUTIONS TO PALÆONTOLOGY

I

LATE TERTIARY FLORAS FROM THE HIGH PLAINS

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With a chapter on the

**LOWER PLIOCENE VERTEBRATE FOSSILS FROM THE OGALLALA
FORMATION (LAVERN ZONE) OF BEAVER COUNTY, OKLAHOMA**

By **CURTIS J. HESSE**

Museum of Paleontology, University of California

With seven plates and eleven text-figures

[Issued October 30, 1936]

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LATE TERTIARY FLORAS FROM THE HIGH PLAINS

INTRODUCTION

Recent field studies by the geological surveys of Kansas and Nebraska have resulted in the discovery of several new and critical occurrences of fossil plants in the Ogallala formation of the High Plains. Certain of these have already been reported by Elias, who is responsible for the discovery and collecting of most of the material which will be discussed in this paper. The plant-bearing deposits of Beaver County, Oklahoma, have been mentioned in print by several authors, as will be described below. It seems desirable to bring together the floral evidence which is now available in this region, where vertebrate faunas have been extensively studied for several decades, but where the plant record has been comparatively unknown.

Most of the important horizons from which fossil vertebrates are collected, in this region and elsewhere, show a striking scarcity of fossil plants. Likewise there is not commonly a complete representation of vertebrate fossils in beds which contain abundant remains of plants. Several reasons for this local incompleteness of the record may be suggested: (1) Mammalian bones occur in most cases in channel deposits in which the sediments are relatively coarse. Under such conditions of deposition, involving a rapid stream current, leaves and all but the larger pieces of wood are likely to be carried away, leaving only the heavier bones to be buried in the sands and conglomerates. Even if deposited, leaves would ordinarily not be well preserved in coarse sediments. The floral record in such situations is limited largely to wood, and to resistant shells of such seeds as the hackberry (*Celtis*). (2) The sediments containing leaf impressions are in all cases fine textured, and for the most part are made up of calcium carbonate, with associated tests of diatoms. They appear to have been deposited in small lakes or pools which occupied temporary basins on the uplands or on floodplains of the streams in whose channels the coarser sediments were accumulated. Such sediments are comparatively rare in the Ogallala formation, and even where present make up only a small part of the section. In most cases they contain leaf impressions. It may be assumed that these lighter structures are floated into the standing water, where they sink and are covered by the fine sediments accumulating in the basins. (3) The habitats occupied by most mammals which enter the fossil record are grasslands, either of prairie or savanna. Conditions there are not suited to the preservation of fossil leaves except in favored and limited situations along the streams. Forests, which have contributed largely to the fossil plant record, were occupied for the most part by small arboreal types of mammals whose remains did not readily enter the sedimentary record, and whose

later Tertiary history is for the most part unknown.¹ The larger types, which visited the forest borders for the purpose of feeding, appear rarely to have died there, or to have been buried in the sediments, along with the leaves which normally accumulate in such situations.

It is not to be expected that the High Plains area will ever furnish such an extensive fossil forest record as that of the later Tertiary in the more humid northern Great Basin and on the Pacific slopes of the Cascades and Sierra Nevada. Climatic conditions east of the Rocky Mountains during the latter half of the Tertiary were such as to limit the distribution of trees to valleys and stream borders, with broad grasslands occupying most of the region. The sediments are generally coarser than those of corresponding age in Oregon and Washington, and even such leaves as were present during their accumulation would not have been readily preserved. The relative importance of vulcanism and the wide occurrence of pyroclastic deposits are important factors in the abundance of fossil plants in the Tertiary of the far western states. The floras herein discussed are therefore especially significant in adding to our knowledge of the vegetation and the physical setting along the east front of the Rockies during later Tertiary time.

The following review of the literature on the fossil plants of this region does not include every reference to their occurrence. We shall endeavor to mention those which constitute the more important contributions to knowledge of later Tertiary vegetation. The extensive discussions of the older Tertiary floras, of which the Fort Union is the most important, will not be considered here, since they involve wholly different plant assemblages and climatic conditions from those of the Miocene and Pliocene epochs. It seems probable that Aughey, in his description of the Miocene and Pliocene floras of northwestern Nebraska,² was referring in part to these older Tertiary floras. Along with *Populus*, *Quercus* and *Salix*, he records *Ficus*, *Liquidambar*, *Sassafras*, palms and other plants which give the assemblage a warm-temperate aspect. Since no fossils were collected by Aughey, and in view of a total absence of such plants in subsequent records, his conclusion that this region was forested by a warm-temperate to subtropical forest during later Tertiary time may be largely disregarded.

The first correct identification of Tertiary *Celtis* stones is that of Engelmann, who points out that seeds from near the forks of Platte River, referred to *Lithospermum*, are in reality those of *Celtis*.³ Since 1902, when Hatcher recorded seeds of *Celtis* in beds ranging in age from the White River formation up into the Loup Fork Miocene of Sioux County, Nebraska,⁴ there have

¹ See Gazin, Jour. Paleon., vol. 9, No. 1, 57-62, 1935; Stock and Furlong, Univ. Calif. Pub. Bull. Dept. Geol. Sci., vol. 13, No. 8, 311-317, 1922.

² Samuel Aughey, *Sketches of the Physical Geography and Geology of Nebraska*, 225, 241-242, 1880.

³ In Simpson, *Report of Explorations across the Great Basin of Utah in 1859*, 261, Govt. Print. Office, 1876. Washington.

⁴ Proc. Amer. Philos. Soc., vol. 41, 126, 1902.

been numerous references to the occurrence of the resistant endocarps of this genus in Tertiary rocks. In 1925, Chaney described as *Celtis hatcheri* material from the White River formation of South Dakota.¹ In the same year Barbour named as the *Hackberry Conglomerate* certain Miocene and Pliocene layers in Custer County and elsewhere in western Nebraska in which endocarps of *Celtis* are so abundant as to make up a conspicuous part of the rock.² Berry also has discussed the stones of *Celtis*, referring to this genus material which had previously been referred to the genus *Tithymalus* of the Euphorbiaceæ.³

The most critical late Tertiary flora previously known from the High Plains is that from Beaver County, Oklahoma. As originally reported by Cragin,⁴ it includes *Credneria daturæfolia*, *Platanus aceroides*, *Populus greviopsis*, *Salix angustata* and *Sapindus* sp. indet. Case records *Ficus*, "*Platinoides*," *Populus*, *Salix* and *Sapindus* as the more abundant genera of these chalk deposits, and mentions the occurrence of mammalian fossils in the overlying sediments.⁵ The portion of his collections deposited at the National Museum have subsequently been described by Berry, who recognized nine forms, including several of the genera listed by earlier workers.⁶ Gould and Lonsdale have included Berry's results in their statement on the Geology of Beaver County.⁷ Further mention will be made below of Berry's conclusions regarding the composition and age of this flora.

In several recent papers,⁸ Elias has described the significant occurrence of grass seeds, boraginaceous nutlets, and remains of a few other prairie plants from many localities in the High Plains, ranging in age from Middle Miocene to Middle or Upper Pliocene. The results of these studies will be considered below.

GEOLOGIC OCCURRENCE OF THE FLORAS

The fossil plants which are discussed in this paper were collected from the Ogallala formation, which builds the gently sloping eastern piedmont of the Rocky Mountains, known as the High Plains. The Ogallala unconformably overlies the lower Miocene Arikaree and still older Tertiary formations in South Dakota, Wyoming, northeastern Colorado and Nebraska, and overlaps truncated beds of Cretaceous and Permian age in southeastern Colorado, New Mexico, Kansas, Oklahoma and Texas. The geographical limits of the High Plains practically coincide with the present distribution of the Ogallala formation.

¹ Carnegie Inst. Wash. Pub. No. 349, 54-56, 1925.

² Nebraska State Mus. Bull., vol. 1, 87-90, 1925.

³ Amer. Mus. Novitates, No. 298, 2, 1928.

⁴ Amer. Geol., vol. 8, 31, 1891.

⁵ Kansas Univ. Quart., vol. 2, 146, 1894.

⁶ Proc. U. S. Nat. Mus., vol. 54, 627-636, 1918.

⁷ Oklahoma Geol. Surv. Bull. 38, 34-35, 1926.

⁸ State Geol. Surv. Kansas, Bull. 18, 150, 1931 (*in* Bull. Univ. Kansas, vol. 32, No. 7); State Geol. Surv. Kansas, Contributions to Paleontology 1, 333-367, 1932 (*in* Bull. Univ. Kansas, vol. 33, No. 10, as Univ. Kansas Sci. Bull., vol. 20, No. 20); Amer. Jour. Sci., vol. 29, 24-33, 1935.

Recent field studies in Nebraska and adjacent territory by Elias, geologist of the Kansas Geological Survey, in cooperation with G. E. Condra and A. L. Lugin of the Nebraska Geological Survey, with R. A. Stirton and his associates of the Museum of Paleontology of the University of California, and with H. J. Cook, have resulted in a zoning of the Ogallala formation by means of seeds of grasses and boraginaceous herbs.¹ The age of the zones is also determined with the aid of previously described and recently discovered vertebrate faunas, especially the horses and beavers, as shown in table 1.² Five, or possibly six, zones of seeds can be recognized in the arenaceous, late Tertiary rocks above the Arikaree. In the latter formation no seeds other than hackberry have been collected. The zones of seeds are as follows, in ascending order:

1. Zone of *Stipidium* α ³ an undescribed species whose minute seeds among the sand grains are barely visible with the naked eye. This zone is the Sheep Creek formation, which outcrops 12 miles south-southeast of Agate, Nebraska. Osborn, Matthew and Cook have referred it to the Middle Miocene. The typical Middle Miocene species of horse, *Merychippus primus*, occurs in the Sheep Creek formation. The thickness of the fossiliferous part of the formation is about 70 feet, below which is an unfossiliferous series about 100 feet thick, lying upon the Arikaree formation.

2. Zone of *Stipidium* $\alpha\alpha$, also an undescribed species, and slightly different from *Stipidium* α . The rocks of this zone are exposed south of Hay Springs, Nebraska. The zone appears to be transitional between the Middle and Upper Miocene, according to the preliminary, unpublished identification by Stirton of a fauna collected by Ted Galusha of Hay Springs. Remains of *Merychippus* are intermediate in size between those of *M. primus* and those of the Upper Miocene *M. isonesus*. The thickness of this zone is probably about 60 feet.

3. Zone of *Stipidium* γ , an undescribed species of a size comparable to the living *Stipa comata*, which is a common grass of western Nebraska. The rocks of this zone, which is about 160 feet thick, are widely exposed along the Niobrara River in Cherry and Brown Counties, Nebraska; along the North Platte River from Bridgeport to Wellen, Nebraska; and at Max on the Republican River, Nebraska. The lower portion falls in the uppermost Upper Miocene, according to an identification by Stirton based on the vertebrates from the lowermost beds of the Ogallala at Valentine, Nebraska. The horses are of the more advanced species, *Merychippus re-*

¹ State Geol. Surv. Kansas. Bull. 18, 150, 1931 (*in* Bull. Univ. Kansas, vol. 32, No. 7); State Geol. Surv. Kansas, Contributions to Paleontology 1, 333-367, 1932 (*in* Bull. Univ. Kansas, vol. 33, No. 10, as Univ. Kansas Sci. Bull., vol. 20, No. 20); Amer. Jour. Sci., vol. 29, 24-33, 1935.

² The faunal data, furnished by R. A. Stirton, has in part been published in the following papers: Teilhard de Chardin and Stirton, Univ. Calif. Pub. Bull. Dept. Geol. Sci., vol. 23, No. 8, 277-290, 1934; Stirton and McGrew, Amer. Jour. Sci., vol. 29, 125-132, 1935; Stirton, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 23, No. 13, 391-485, 1935; Stirton, *Succession of North American Continental Pliocene Mammalian Faunas*, Amer. Jour. Sci., vol. 32, 1936.

³ Elias, Amer. Jour. Sci., vol. 29, 28, fig. A, 1935.

publicanus and *M. (Protohippus) perditus*, the latter occurring also in the Upper Miocene Barstow of California. A primitive beaver referred to the genus *Monosaulux* is also present. Some of these faunas are regarded by the Nebraska Geological Survey as Lower Pliocene, but Stirton¹ considers them as transitional between Upper Miocene and Lower Pliocene. To the lower part of this zone, and slightly below the fauna regarded by Stirton as transitional, belongs in all probability the horizon in Brown County, Nebraska, from which fossil leaves have been collected, as discussed below.

TABLE 1—Sequence of Mammalian and Plant Remains in the High Plains

Age	Zone	Seeds	Leaves	Horse	Beaver
Middle Pliocene	5	<i>Panicum elegans</i> <i>Biorbia fossilia</i> (= <i>B. rugosa</i>) <i>Krynitzkia chaneyi</i>	Logan County Flora	<i>Neohipparion</i> <i>Nannippus cf.</i> <i>lenticulare</i>	<i>Dipoides</i>
Transitional between Lower and Middle Pliocene	4	<i>Krynitzkia coroniformis</i>	Beaver County Flora	<i>Neohipparion</i> <i>Nannippus</i>	<i>Eucastor</i>
Uppermost Upper Mio- cene, or transitional with Lower Pliocene	3	<i>Stipidium</i> γ	Brown County Flora	<i>Merychippus</i> <i>republicanus</i> <i>M. (Protohippus)</i> <i>perditus</i>	<i>Monosaulux</i>
Transitional between Middle and Upper Miocene	2	<i>Stipidium</i> αα		<i>Merychippus</i>	
Middle Miocene	1	<i>Stipidium</i> α		<i>Merychippus</i> <i>primus</i>	

4. Zone of *Krynitzkia coroniformis*.² To this zone belong the uppermost 20 or 30 feet of the Ogallala exposed at Valentine, Nebraska. The vertebrates from these beds at Valentine are considered by Stirton³ as transitional from Lower to Middle Pliocene. *Neohipparion* and *Nannippus* are the representatives of the horses at this level, and the beaver, *Eucastor*, is also included in the fauna. These genera, and others transitional between the Lower and Middle Pliocene, have recently been collected at the fossil plant locality in Beaver County, Oklahoma. They are also included in the Clarendon fauna of western Texas. The complete zone is about 100 feet thick and is elsewhere exposed along the North Platte River from

¹ Stirton and McGrew, *op cit.* 129.

² Elias, State Geol. Surv. Kansas, Contributions to Paleontology 1, 356, 1932 (in Bull. Univ. Kansas, vol. 33, No. 10, as Univ. Kansas Sci. Bull., vol. 20, No. 20).

³ Stirton and McGrew, *op. cit.* 131.

Bridgeport to Lewellen, Nebraska, at McCook, Nebraska, and in north-western Kansas.

5. Zone of *Biorbia fossilia* (= *B. rugosa*),¹ with a lower subzone of *Krynitzkia chaneyi*² and an upper subzone of *Panicum elegans*.³ This zone belongs to the Middle Pliocene, the age being determined by the fauna at Long Island, Kansas (Sternberg's quarry), which is located in the lower subzone. A recently discovered fauna in this zone from the type-locality of the Ogallala, northeast of Ogallala, Nebraska, also of Middle Pliocene age, has recently been described by Hesse⁴ of the University of California. The horses of these faunas are a more advanced species of *Hipparion* and *Nannippus* cf. *lenticulare*. *Dipoides*, an advanced type of beaver, also occurs here. The thickness of the zone is about 100 feet. It is widely distributed in southwestern and south central Nebraska, in southeastern Wyoming, northeastern Colorado, western Kansas, the Panhandle of Oklahoma, and east of Darrouzet, northern Texas.

The leaves from Logan County, Kansas, belong to this zone, the correlation being based on the vertebrates from sands directly below the leaf-bearing diatomaceous marl. This is the "Rhinoceros Hill" fauna of H. T. Martin.

6. Zone of *Echinochloa* n. sp., undescribed. The rocks of this zone are exposed at North Platte, Nebraska. No vertebrates have been discovered in these rocks, but from the general geologic position of the exposures, the suggestion is made that these rocks belong to Upper Pliocene. The association in them of *Echinochloa* with *Panicum elegans* and the absence of such other seeds as the common Middle Pliocene *Biorbia fossilia* are in accord with this age reference. The thickness of this zone is probably about 175 feet. South and southwest of Nebraska, it appears to be represented by the algal (*Chlorellopsis*) limestone, which caps the Ogallala formation in northeastern Colorado, northwestern Kansas, the Panhandle of Oklahoma, northern Texas and northeastern New Mexico.⁵

The fossil plants described in this paper come from four localities, as follows:

1. PLUM CREEK, NORTHWESTERN BROWN COUNTY, NEBRASKA.

The leaves were found in a one-foot bed of clayey, diatomaceous marl about half a mile below the dam of the power house on the right side of Plum Creek. At this exposure, known as White Cliffs, the diatomaceous marl lies in the lower part of the section, some 80 feet above the water-level

¹ Elias, State Geol. Surv. Kansas, Contributions to Paleontology 1, 350, pl. 29, figs. 2a-e, 1932 (*in* Bull. Univ. Kansas, vol. 33, No. 10, as Univ. Kansas Sci. Bull., vol. 20, No. 20).

² *Ibid.* 357, pl. 30, figs. 4a-d.

³ *Op. cit.* 342, pl. 28, figs. 2a-c and 4.

⁴ Univ. Kansas Sci. Bull., vol. 22, No. 5, 79-117, 1935 (*in* Bull. Univ. Kansas, vol. 34, No. 8).

⁵ The wide distribution of the algal limestone in the last two states has been recently established by Chas. V. Theis of the U. S. Geological Survey, who has submitted his samples of the rock to Elias for examination.

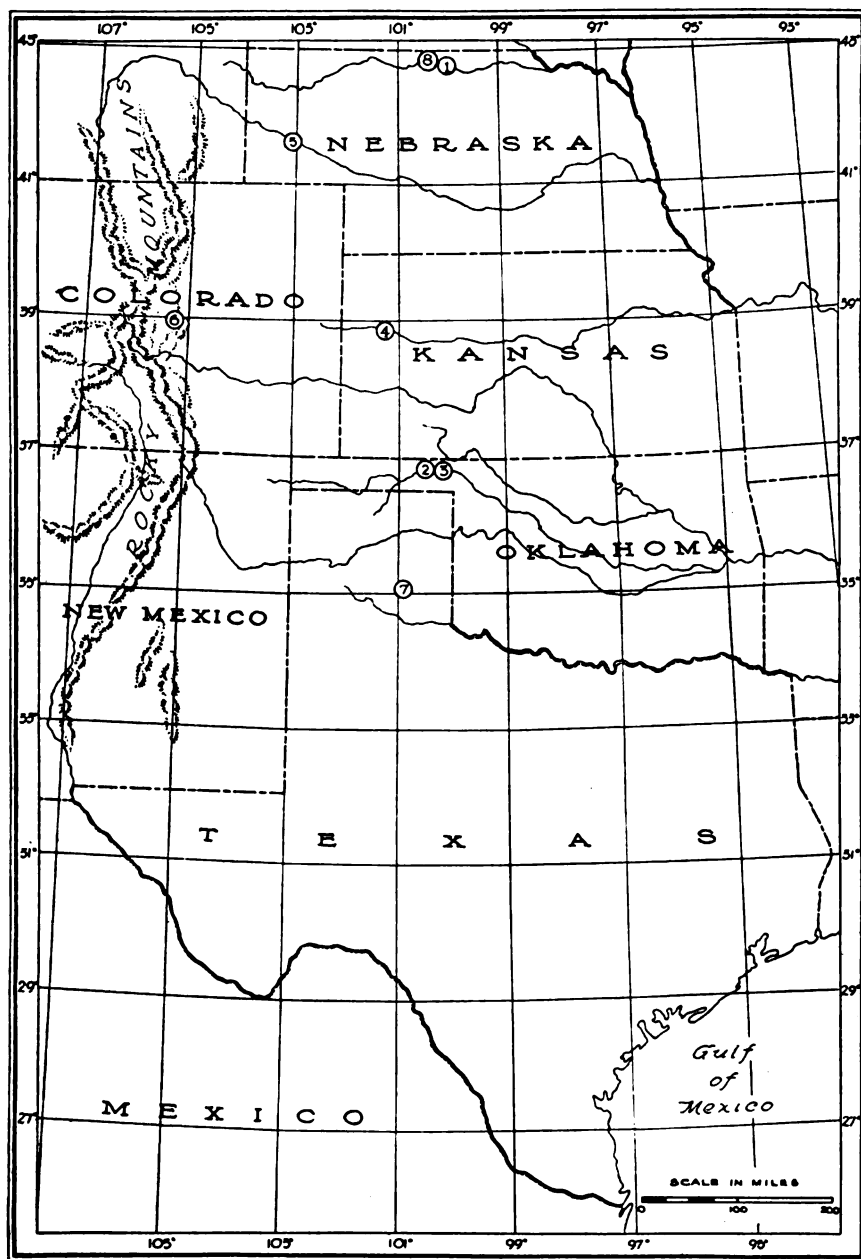


FIG. 1—1—White Cliffs locality on Plum Creek, northwestern Brown County, Nebraska (Locality P-54).

2—Southwest of Beaver, Beaver County, Oklahoma (Locality P-42).

3—Southwest of Beaver, Beaver County, Oklahoma (Locality P-44), about 3½ miles east of Locality P-42.

4—East of Marshall Ranch on the north fork of Smoky Hill River, Logan County, Kansas (Locality P-43).

5—Eight miles north of Bridgeport, Morrill County, Nebraska.

6—Florissant, Colorado.

7—Shannon Ranch locality, near Clarendon, Donley County, Texas.

8—Mossman Ranch locality, near Valentine, Cherry County, Nebraska.

of the creek. The total thickness of the exposed Ogallala at this point is about 200 feet. No seeds other than hackberry stones have been found in this exposure, and no vertebrate remains are known from it or from other near-by outcrops of the Ogallala. Two hundred yards up the creek and on the same side, an erect silicified tree stump of *Platanus*, presumably representing the leaf species, *P. aceroides*, has been dug out by C. R. Taylor, superintendent of the power house. Leveling has shown that the position of this log is at about the elevation of the leaf-bearing diatomaceous marl.

Following is the list of species which have been collected at this locality:

Cyperacites sp.	Salix coalingsensis
Fraxinus ungeri	Typha lesquereuxi
Platanus aceroides	

In addition there is an extensive diatom flora which will be discussed below.

This is locality P-54 in the series of the Geological Survey of Kansas (See ①, figure 1).

A correlation of the Brown County horizon with that described by Stirton and McGrew from Cherry County, Nebraska, on the basis of mammalian fossils, has already been suggested. The recent determination by Daugherty of wood from the Mossman Ranch, in Cherry County (see ⑧, figure 1), as that of *Platanus*, and of wood from the same horizon, one-fourth of a mile west of the railroad locality, as that of *Populus*, is in complete agreement with this correlation. Leaves and wood of *Platanus* have been found at the Brown County locality, and leaves of *Populus* have been recorded from other, somewhat younger horizons at localities to the south. The wood of *Hamamelis* has also been recognized by Daugherty, from the Mossman Ranch locality. This genus has not previously been reported as a fossil in North America, although several species of *Hamamelites* have been recognized in Cretaceous and Eocene deposits.

2 and 3. SOUTHEAST OF BEAVER, BEAVER COUNTY, OKLAHOMA.

Two different kinds of late Tertiary rocks are exposed in Beaver County. The rocks in which the leaves and vertebrates have been collected are exposed in a topographically lower part of the county, along the lower courses of the tributaries to Beaver River, which traverses the county in an east-west direction. The leaves were collected in the light-buff to nearly white, diatomaceous marl, which has locally been altered to flint. The best preserved leaves and seeds were collected in this flint. Remains of vertebrates were collected from sandy clay and loam directly above the diatomaceous marl, and from a sandy layer approximately 8½ feet below.

In the high dissected plateau of the southern part of the county and the adjacent part of Texas, another type of Tertiary rocks is exposed. Here the most common rocks are sands and grits, which are capped by the algal (*Chlorellopsis*) limestone, identical with that described from northwestern Kansas and northeastern Colorado.¹ In the grits near Darrouzett, Texas, *Biorbia fossilia* and an undescribed species of *Berriochloa* have been collected. These seeds indicate Middle Pliocene age for the rocks.

Although no direct contact between the high- and low-land Tertiary has been observed, their relative elevation leaves no doubt about the older age of the leaf- and vertebrate-bearing beds. Plant fossils occur at two localities

¹ State Geol. Surv. Kansas, Bull. 18 (in Bull. Univ. Kansas, vol. 32, No. 7), 1931.

in the lowlands. The earlier collection made by Case and deposited at the University of Kansas and at the National Museum came, in all probability, from the large exposure of diatomaceous marl in the center of Section 3, Range 25 East, Township 3 North. This is locality P-42 in the series of the Geological Survey of Kansas. (See ②, figure 1.)

In addition to the diatoms, which will be listed below, the following species have been recognized:

<i>Celtis kansana</i>	<i>Platanus aceroides</i>
<i>Cercidiphyllum crenatum</i>	<i>Salix coalingensis</i>
<i>Cyperacites</i> sp.	<i>Sapindus oklahomensis</i>
<i>Diospyros pretexana</i>	<i>Typha lesquereuxi</i>
<i>Fraxinus ungeri</i>	<i>Ulmus moorei</i>
<i>Gymnocladus casei</i>	

The University of Kansas expedition of 1933 collected vertebrates in sandy clay directly above the diatomaceous marl at this locality. More recently additional mammalian remains have been secured by Stirton both from above and below the leaf-bearing bed. These collections have been studied by C. J. Hesse of the University of California, who has written a chapter included in this paper. The few fragmentary leaves collected in the diatomaceous marl are similar to those in the Case collection.

Well-preserved leaves and seeds were collected by Elias $3\frac{1}{2}$ miles east of the preceding locality, in about the center of Section 5, Range 26 East, Township 3 North. This is locality P-44 in the series of the Geological Survey of Kansas. (See ③, figure 1.) Here a bed of flint caps the diatomaceous marl, and contains the following species:

<i>Acer negundoides</i>	<i>Platanus aceroides</i>
<i>Bumelia oklahomensis</i>	<i>Populus lamottei</i>
<i>Cercidiphyllum crenatum</i>	<i>Salix coalingensis</i>
<i>Cyperacites</i> sp.	<i>Sapindus oklahomensis</i>
<i>Diospyros pretexana</i>	<i>Typha lesquereuxi</i>
<i>Gymnocladus casei</i>	

4. EAST OF MARSHALL RANCH ON NORTH FORK OF SMOKY HILL RIVER, LOGAN COUNTY, KANSAS.

The exposures of diatomaceous marl at this locality extend along the south side of Smoky Hill River for about $3\frac{1}{2}$ miles in Wallace and Logan Counties. Fossil leaves were collected from only a single exposure, which is in Logan County about one-fourth of a mile east of the Wallace County line. Previously only one fragment of a leaf had been found and described from this place.¹ In 1933 a layer of fossiliferous, somewhat clayey, diatomaceous marl one foot thick was discovered at about the middle of a diatomaceous bed 11 feet in thickness. The leaves were found scattered in this layer, and are accompanied by well-preserved remains of fresh-water fishes. These specimens were collected chiefly by Joe DeTilla of Wallace, and by Claude Hibbard of the University of Kansas.

In the sand directly below the diatomaceous marl numerous mammalian fossils have previously been collected by H. T. Martin and his associates of the Museum of Natural History, University of Kansas. The age of this fauna, which has never been described,² is now considered by Stirton to be

¹ Elias, State Geol. Surv. Kansas, Contributions to Paleontology 1, 340, pl. 30, figs. 7a, 7b, 1932 (in Bull. Univ. Kansas, vol. 33, No. 10, as Univ. Kansas Sci. Bull., vol. 20, No. 20).

² See complete list of identified species compiled by H. T. Martin for "Geology of Wallace County," Elias, State Geol. Surv. Kansas, Bull. 18, 160-161, 1931 (in Bull. Univ. Kansas, vol. 32, No. 7).

Middle Pliocene.¹ The leaves from the overlying diatomaceous marl are apparently of the same age. They include the following species:

Celtis kansana
Cyperacites sp.
Populus lamottei

Salix coalingensis
Typha lesquereuxi
Ulmus moorei

This is locality P-43 in the series of the Geological Survey of Kansas. (See ④, figure 1.)

The list of the diatoms will be given below.

From two other localities in the High Plains, small collections of plant fossils have been secured. One of these is in northwestern Nebraska, in beds commonly considered to be of Lower Miocene age. The exact description of the locality is as follows: 8 miles north of Bridgeport, Morrill County, Nebraska, in Section 16, Range 50 West, Township 21 North. (See ⑤, figure 1.) Poorly preserved leaves of a willow not determinable as to species but resembling *S. coalingensis* occur here, together with stem fragments. Due to the unfavorable character of the matrix, which is a fine, rather friable sand, the plant record at this point is necessarily incomplete. As now known it can not be considered to have any important bearing on the general problems of the age and physical significance of the other floras of the High Plains. An associated mammalian fauna is now being studied by C. B. Schultz of the University of Nebraska, and by C. Frick of the American Museum of Natural History.

A second locality is in western Texas, where R. A. Stirton has secured wood of *Fraxinus*, palm seeds, and a seed of *Arctostaphylos*, in association with an extensive mammalian fauna from the Clarendon beds. The exact description of the locality is as follows: 10 miles north of Clarendon and approximately 1¾ miles northwest of Goldston, on the old F. W. Shannon Ranch, Donley County, Texas, in Section 42, Block C-3. (See ⑦, figure 1.) The age of the fauna, as determined by Stirton,² is late Lower Pliocene. The age of the flora, as recently determined by Mason, is close to that found in the Ricardo formation of California, which is referred to the Lower Pliocene.³

AGE OF THE HIGH PLAINS FLORAS

While there is a general resemblance between the floras from Nebraska, Kansas and Oklahoma, as above listed, certain significant differences are apparent, both in their composition and leaf character, which indicate that they are not of exactly the same age at all of the localities where they have been collected. These differences in age are in accord with the evidence of mammalian faunas and seeds from associated or adjacent horizons, as shown in table 1. There is no basis at present for postulating a phylo-

¹Oral communication to M. K. Elias by R. A. Stirton.

²Stirton, Amer. Jour. Sci., vol. 32, 1936.

³Webber, Carnegie Inst. Wash. Pub. No. 412, 1933.

genetic trend for the leaves of fossil spermatophytes through the Tertiary, such as has been suggested for fossil mammals and grass seeds. On the contrary, there is accumulating evidence for the belief that forest floras have retained certain of their dominant genera and species throughout much of the Tertiary, and that some of these floras have survived in modified form down to the present. In all cases where such modern plant assemblages have been studied, and compared with corresponding units of the Tertiary, there are various characters by which they may be distinguished. The species are different in many, or perhaps in most cases, and genera have been added and eliminated. None the less, definite relationships are apparent between fossil floras of different ages and between fossil and living floras—relationships which suggest that they have moved southward across western North America, from Alaska to Mexico and Central America, during the Cenozoic Era. This being the case, an important basis for determining the relative age of many Cenozoic floras lies in a determination of their changes in distribution.

Unlike certain marine formations, which are widely and almost continuously distributed over extensive areas, the deposition of many terrestrial formations, including the Ogallala, appears to have been distinctly local. There is a further difference involving time duration; whereas some horizons of the Paleozoic may be judged, from their thickness, to have been deposited over long ages, certain terrestrial deposits of the Tertiary are considered to represent only a small fraction of that time. Clearly the problems of the palæontologist at these later levels must often be solved through the use of different, or at least modified, criteria as compared with those employed in age determinations of older strata. It is the purpose of this discussion to demonstrate that the floras from the High Plains are of younger age, even though containing many of the same plants, than those from the northern part of the Great Basin. It will further be shown that the floras within the High Plains, although including many of the same species, vary somewhat in age, depending upon their geographic occurrence and other factors. The age relations of the High Plains floras will be considered separately for the three regions and horizons represented.

THE FLORA FROM BROWN COUNTY, NEBRASKA

Only five types of plants have been recognized here, of which *Cyperacites* is too indefinite systematically to carry any weight in age determination. Of the remaining species, *Fraxinus ungeri* and *Typha lesquereuxi* have been recorded from the Florissant beds of Miocene age (see ⑥, figure 1); *Platanus aceroides*¹ and *Typha lesquereuxi* occur regularly in the Mascall of the Great Basin, which is of Upper Miocene age. Only one species, *Salix coalingsensis*, is typically Pliocene, and even it is represented by related leaves in the Upper Miocene. As far as it goes, the evidence of the Brown

¹ In that region more commonly known as *P. dissecta*.

County plants favors their reference to the Upper Miocene; but it is clear that no final conclusions can be reached regarding the age of a flora containing so few species, especially when several of them are no more distinctive stratigraphically than *Platanus aceroides* and *Typha lesquereuxi*.

From various localities in Nebraska, Elias has collected seeds of a grass, *Stipidium* γ, which he refers to Zone 3 as indicated in our discussion of the geologic occurrence of the floras. The leaf-bearing deposits in Brown County fall in the lower part of this zone whose age is indicated as transitional between Upper Miocene and Lower Pliocene on the basis of associated vertebrates.

There is associated with the leaf fossils at the Brown County locality a diatom flora which has been studied by K. E. Lohman. The 31 species represented, together with those of other diatom floras from critical localities in these High Plains, are shown in table 2. All of these data have been

TABLE 2—Distribution of diatoms in the High Plains deposits.

Species	Brown County Loc. P-54*	Beaver County Loc. P-42§	Logan County Loc. P-43†
<i>Amphiprora alata</i> (Ehrenberg) Kützing.....			F
<i>Amphora ovalis</i> Kützing.....			F
<i>Amphora</i> cf. <i>A. rheinoldii</i> Hanna.....			R
<i>Amphora</i> cf. <i>A. veneta</i> Kützing.....			R
<i>Anomæoneis sphærophora</i> (Kützing) Pfitzer.....	F		C
<i>Anomæoneis</i> sp.....		F	
<i>Biddulphia levis</i> Ehrenberg.....	R		
<i>Caloneis bacillum</i> (Grunow) Mereschkowsky.....		R	
<i>Caloneis bivittata</i> Pantocsek.....	R		
<i>Caloneis silicula tumida</i> Hustedt.....		F	
<i>Caloneis</i> cf. <i>C. formosa</i> (Gregory) Cleve.....			R
<i>Cocconeis placentula</i> Ehrenberg.....			F
<i>Cyclotella</i> cf. <i>C. meneghiniana</i> Kützing.....			A
<i>Cyclotella</i> ? n. sp.....		R	
<i>Cymatopleura</i> sp.....		F	
<i>Cymbella aspera</i> (Ehrenberg) Cleve.....			F
<i>Cymbella cistula</i> (Hemprich) Grunow.....	C		
<i>Cymbella cuspidata</i> Kützing.....	F		
<i>Cymbella erhenbergii</i> Kützing.....	F	C	
<i>Cymbella lanceolata</i> (Ehrenberg) Van Heurck.....		C	
<i>Cymbella mexicana</i> (Ehrenberg) Cleve.....			F
<i>Cymbella parva</i> (Wm. Smith) Schmidt.....			F
<i>Cymbella turgida</i> (Gregory) Cleve.....			F
<i>Cymbella ventricosa</i> Kützing.....		R	F
<i>Cymbella</i> cf. <i>C. cuspidata</i> Kützing.....		R	
<i>Cymbella</i> cf. <i>C. cymbiformis</i> (Agardh? Kützing) Van Heurck.....		R	
<i>Cymbella</i> cf. <i>C. helvetica</i> Kützing.....		F	
<i>Denticula elegans</i> Kützing.....			A
<i>Diatoma vulgare ehrenbergii</i> Grunow.....		C	
<i>Diatoma</i> sp.....	R		
<i>Eunotia pectinalis</i> (Kützing) Rabenhorst.....	F		
<i>Eunotia prærupta</i> Ehrenberg.....	F	F	
<i>Fragilaria construens</i> (Ehrenberg) Grunow.....	C		
<i>Fragilaria pinnata</i> Ehrenberg.....	C	F	
<i>Fragilaria</i> sp.....		F	

TABLE 2—Distribution of diatoms in the High Plains deposits.—Continued

Species	Brown County Loc. P-54*	Beaver County Loc. P-42§	Logan County Loc. P-43†
<i>Frustulia rhomboides</i> (Ehrenberg) De Toni.....			F
<i>Gomphonema intricatum</i> Kützing.....	F	F	
<i>Gomphonema lanceolatum insignis</i> (Gregory) Cleve.....	F		
<i>Gomphonema semiapertum</i> Grunow.....		F	F
<i>Hantzschia amphioxys</i> (Ehrenberg) Grunow.....	F		F
<i>Hantzschia amphioxys vivax</i> (Hantzsch) Grunow.....			
<i>Melosira italica</i> (Ehrenberg) Kützing.....	C	A	
<i>Melosira undulata</i> (Ehrenberg) Kützing var.....	F		
<i>Melosira</i> n. sp. aff. <i>M. granulata spiralis</i> Kützing.....		A	
<i>Navicula ambigua</i> Ehrenberg.....	R		
<i>Navicula anglica</i> Ralfs.....		F	
<i>Navicula bacillum</i> Ehrenberg.....	C	R	
<i>Navicula citrus</i> Krasske.....	F		
<i>Navicula cuspidata</i> Kützing.....		R	
<i>Navicula dicephala</i> (Ehrenberg) Wm. Smith.....	F	C	
<i>Navicula tuscula</i> Ehrenberg.....	F		
<i>Navicula</i> n. sp. aff. <i>N. peregrina</i> (Ehrenberg) Kützing.....		F	
<i>Navicula</i> n. spp. A-D.....		F-C	
<i>Navicula</i> sp.....	F	C	F
<i>Neidium iridis ampliatus</i> (Ehrenberg) Cleve.....		R	
<i>Nitzschia spectabilis</i> Ralfs.....		F	
<i>Nitzschia</i> sp.....		R	F
<i>Pinnularia borealis</i> Ehrenberg.....	F		
<i>Pinnularia fasciata</i> (Lagerstedt) Hustedt.....		R	
<i>Pinnularia mesolepta</i> (Ehrenberg) Wm. Smith.....	R		
<i>Pinnularia microstauron</i> (Ehrenberg) Cleve.....	F	C	F
<i>Pinnularia nobilis</i> Ehrenberg.....	F		
<i>Pinnularia viridis sudetica</i> (Hilse) Hustedt.....			F
<i>Pinnularia</i> cf. <i>P. nobilis</i> Ehrenberg.....		R	
<i>Pinnularia</i> cf. <i>P. viridis</i> (Nitzsch) Ehrenberg.....			F
<i>Pinnularia</i> n. sp.....		R	
<i>Stauroneis anceps</i> Ehrenberg.....	F		
<i>Stauroneis phoenicenteron</i> Ehrenberg.....		F	
<i>Stauroneis</i> cf. <i>S. parvula</i> Grunow.....		F	
<i>Surirella ovata</i> Kützing.....	F		R
<i>Surirella</i> cf. <i>S. striatella</i> Turpin.....			F
<i>Surirella</i> sp.....		R	
<i>Synedra ulna</i> (Nitzsch) Ehrenberg.....	F		
<i>Synedra</i> cf. <i>S. ulna</i> (Nitzsch) Ehrenberg.....			R
<i>Tetracyclus lacustris</i> Ralfs.....	F		
<i>Tetracyclus pagesi</i> Heribaud.....		F	
<i>Tetracyclus</i> sp.....	F		
Total species.....	31	37	25

NOTE: A, abundant; C, common; F, few; R, rare.

* This is U.S.G.S. Diatom Locality 2718.

§ This is U.S.G.S. Diatom Locality 2750.

† This is U.S.G.S. Diatom Locality 2716.

made available through the courtesy of Mr. Lohman and the United States Geological Survey. Regarding the diatoms from the Brown County locality, Lohman has stated¹ that they are similar to those obtained from diatomite near Valentine, Cherry County, Nebraska. From these beds, associated

¹ Letter of September 3, 1935.

mammalian fossils, comprising the Niobrara River fauna, are considered by Stirton to be transitional between the Upper Miocene and Lower Pliocene, but nearer to the Miocene than the Pliocene.¹ Lohman concludes, regarding the diatom flora from Brown County: "... this flora contains some species which are in the Mascall formation of eastern Oregon, but there is such a general dissimilarity between the two that no correlation with the West Coast floras can be made. The similarity between the flora from sample P-54 (Brown County) and the flora from near Valentine is, however, very great, and more assurance is felt in correlating the two. Many lines of evidence suggest that the Mascall formation is older than any of the floras here under discussion." The indications of the diatom flora and the mammalian fauna are therefore in accord in placing the age of the beds containing the Brown County flora as latest Miocene or transitional between the Miocene and the Pliocene.

As will be more fully discussed in a later chapter, the habitat suggested by the Brown County plants is of a much drier type than that indicated by the Mascall flora in the northern Great Basin. The small number of species is in itself suggestive of a habitat unfavorable for forests of the type which characterized the Mascall. The three trees of the Brown County flora, ash, sycamore and willow, are today widely distributed on stream borders in semiarid regions, where the more mesic element, including such common Mascall genera as alder, elm, hickory, maple and redwood, is entirely absent. Having in mind the general trend toward aridity through the Tertiary, the more xeric character of the Brown County flora and its more southern position as compared to the Mascall are in accord with the evidence of the diatoms and the mammals in suggesting an age younger than the Mascall and intermediate between the Miocene and Pliocene.

THE FLORA FROM BEAVER COUNTY, OKLAHOMA

The fossil plants from Beaver County are more numerous as individuals and species than from any other locality in the High Plains. Reference to table 3, showing the local occurrence of the species in the High Plains floras and their representation outside this area, indicates the presence in this Oklahoma assemblage of all of the species recorded from Brown County. This table suggests the Upper Miocene relationships of the Beaver County flora. Four species are common to the Mascall and related floras of the northern Great Basin. Of these, *Typha lesquereuxi* can not be said to be of critical value in correlation, since it represents the leaves of a type of cattail which ranges from the Lower Miocene into the Pliocene; these leaves are not sufficiently well-preserved to be distinguishable from those of the living *T. latifolia*. The presence of *Platanus aceroides* in the Beaver County flora has likewise no great age significance. This species has been reported from the lowermost Eocene to the Miocene, and its leaves are not essen-

¹ Stirton and McGrew, Amer. Jour. Sci., vol. 29, 131, 1935.

tially different from those of the living *P. occidentalis*. The Beaver County material should probably be referred to the typically Miocene species, *P. dissecta*; but even the leaves of this relatively well-defined sycamore are not readily distinguishable from those of the living eastern species; and although *P. paucidentata* of the Pliocene is definitely more deeply and more slenderly lobed, with fewer teeth, at least one of the specimens figured by Dorf from the Sonoma Tuff seems to resemble our material. *Acer negundoides* has not previously been reported outside of the Upper Miocene of the Great Basin region; because of its relationship to the living *A. negundo*, this fossil species may be expected to occur regularly in the Pliocene, where climatic conditions in western America, as now known, were well suited to the box-elder. *Cercidiphyllum crenatum* has never before been recorded in

TABLE 3—Local distribution and outside occurrence of the High Plains Flora.

	Brown Co., Nebraska Locality P-54	Beaver Co., Oklahoma Locality P-42	Beaver Co., Oklahoma Locality P-44	Logan Co., Kansas Locality P-43	Miocene		Pliocene	
					Florissant	Mascall and related floras of northern Great Basin	Esmeralda	California Pliocene
<i>Acer negundoides</i>			X			X		
<i>Bumelia florissanti</i> ..			X		X			
<i>Celtis kansana</i>		X		X				
<i>Cercidiphyllum crenatum</i>		X	X			X		
<i>Diospyros pretexana</i> .		X	X					
<i>Fraxinus ungeri</i>	X	X			X			
<i>Gymnocladus casei</i> ...		X	X		X			
<i>Platanus aceroides</i> ...	X	X	X			X		
<i>Populus lamottei</i>			X	X				
<i>Salix coalingensis</i>	X	X	X	X			X	X
<i>Sapindus oklahomensis</i>		X	X					
<i>Typha lesquereuxi</i> ...	X	X	X	X	X	X	X	
<i>Ulmus moorei</i>		X		X				X
Total species: 13...	4	10	10	5	4	4	2	2

beds younger than the Upper Miocene. Its testimony as to the Miocene age of the Beaver County flora carries more weight than that of any of the other species mentioned, since the genus is now confined to Asia, and since the Asiatic element, of which it was a member, was largely eliminated from North American floras at the close of the Miocene.

In addition to these 4 species which are known to occur in Miocene or older rocks, there are 5 others in the Beaver County flora which are closely

related to Miocene species of their genera. *Celtis kansana* differs only in minor respects from the Lower Miocene *C. obliquifolia* of eastern Oregon. Although leaves of this genus are not commonly reported at younger Tertiary horizons, the presence of seeds has been recorded from all of the series in the Great Plains, after and including the Oligocene. *Fraxinus ungeri* has leaflets resembling *F. denticulata* as represented in the Lower Miocene of eastern Oregon, and it is a question whether there is more than a geographic basis for keeping these two species distinct. The same is true of *Sapindus oklahomensis*, which differs from *Sapindus oregonianus*, the Upper Miocene species of the northern Great Basin, only in its somewhat smaller size and more slender shape. *Salix coalingsensis*, while confined to the Pliocene, has several corresponding species in the Miocene of western America, as mentioned in the discussion of its systematic relationships. *Ulmus moorei* closely resembles *U. brownellii* from the Lower Miocene of eastern Oregon; there is a critical resemblance in its commonly simple-serrate margin, but it differs in being smaller and less slender. The evidence of these 5 species throws added weight toward the suggestion that the Beaver County flora may be as old as Upper Miocene.

The age of the Florissant flora is commonly considered to be Miocene, although opinions differ as to whether it is referable to the lower or upper part of this series. The presence of a large number of genera (even omitting many obviously incorrect identifications), which are associated with mild, humid habitats, suggests that it may properly be referred to the Lower Miocene. A recent suggestion, based on vertebrate evidence,¹ calls for an even greater age for the Florissant beds. On the other hand, the associated grasses are considered by Elias to represent a late Miocene or Pliocene age. Only 3 species from Beaver County are included in the list from Florissant. One of these is *Typha lesquereuxi*, whose stratigraphic value as above stated is slight. The others, *Bumelia florissanti* and *Fraxinus ungeri*, have not been reported in beds other than the Florissant. Another Florissant species, *Rhamnus lesquereuxi*, has been recognized by Berry as present in the Beaver County flora. An examination of Berry's type gives the writers no basis for including this species in the floral list, since we find no distinction between it and *Gymnocladus casei*. The corresponding material from Florissant, described by Lesquereux as *Rhamnus notatus* (?),² appears also to be referable to *Gymnocladus casei*. But since the specimen has not as yet been examined, it is not possible to state certainly that *Gymnocladus casei* was present at Florissant. There are in addition, 3 species at Beaver County which are obviously related to those from Florissant. The Florissant species, *Celtis mccoshii*, shows no resemblance to *C. kansana* from Beaver County, but one of the leaves described from the Colorado flora as *Fraxinus heeri* appears to be referable to *C. kansana*. No less than 5 species of *Sapindus* have been

¹ Gazin, Jour. Paleont., vol. 9, No. 1, 1935.

² U. S. Geol. Surv. Terr., Rept., vol. 8, 189, pl. 38, fig. 15, 1883.

described from the Florissant beds. It is quite impossible to demonstrate that our Beaver County specimens of this genus are specifically distinct from one or more of these. As above discussed, *Ulmus moorei* is definitely related to *U. brownellii*, which occurs at Florissant as well as in eastern Oregon.

Summarizing the resemblances of the Oklahoma material to the Miocene, there are 4 species identical and 5 related to those of the northern Great Basin; 3 species are identical and 3 related to those of the Florissant. The Florissant flora, although geographically nearer to Beaver County, may be somewhat older than the related floras from the Great Basin. Another possible explanation for its less close resemblance to the Beaver County flora may lie in habitat differences. The Florissant flora appears to have occupied a relatively high altitude, while both the Great Basin Miocene and Beaver County floras are considered to have lived within a few hundred feet of sea-level.

No discussion of relationships between fossil floras can be complete without a consideration of their differences as well as their similarities. The Beaver County flora contains 2 species, *Diospyros pretexana* and *Populus lamottei*, which are unlike those representing their genera in the Miocene of western America. Both of these Beaver County species appear to be relatively modern, in that their leaves suggest an adaptation toward lessened humidity. The leaves of *Diospyros pretexana* are, as the name implies, similar to those of the living *D. texana*, which occupies prairie borders, dry rocky mesas, and isolated canyons in the southwestern interior. The larger leafed *D. virginiana*, ranging over the more humid states to the east, finds its Tertiary equivalents in species whose leaves are of comparable size and definitely larger than those from Beaver County. Leaves of the cottonwood type are rare in the fossil record, with *Populus richardsoni* from the Upper Miocene at Elko, Nevada, and *P. prefremontii* from the Pliocene of California representing the only well-defined species. Still another Beaver County species, *Gymnocladus casei*, is not even generically represented in Miocene and older floras of western America, unless the material referred by Lesquereux to *Rhamnus notatus* (?) represents *Gymnocladus casei*, which seems probable. The suggestion may be made that its absence to the north is due to a southern origin and that it had only reached the latitude of Oklahoma or Colorado by later Tertiary time.

An even more significant difference between the Beaver County flora and those of Miocene age from Colorado and the northern Great Basin lies in the absence from it of certain characteristic elements. The more significant of these is the redwood element which is so wide-spread in the Miocene of western America. *Sequoia*, *Alnus*, *Quercus* (of the *Lithocarpus* type), *Acer* (of the broad-leafed type) and *Umbellularia* are among the genera which are commonly present in Miocene floras of western America. Their absence at Beaver County carries the same suggestion regarding climatic change as

the presence there of distinctive species of *Diospyros* and *Populus*. This suggestion of lessening humidity is consistent with an assumption of younger age, since there is a definitely established trend toward aridity in the record of the Tertiary both in western America and in eastern Asia. The absence of the Miocene oak border element from the Beaver County flora is also noteworthy. The live-oak and other evergreen members of this element have never become established in the High Plains, and at the present time are for the most part localized on the Pacific Coast. A possible cause for the absence of the broad-leaved deciduous oaks will be discussed below. The paucity of the Asiatic element, already mentioned in the discussion of *Cercidiphyllum*, is another indication of late Tertiary age, since this element is abundant in all of the older Tertiary floras of western America, persisting into the Upper Miocene.

In summary, we may conclude that while there are numerous Beaver County species, making up more than 75 per cent of the total, which are identical with or closely related to the plants from the Miocene of western America, there are marked differences which indicate environmental dissimilarity and presumably a discrepancy in age.

In his study of the Beaver County flora,¹ Berry reaches the tentative conclusion that it is of Upper Miocene age. He recognizes several species which are identical with or similar to those from the Miocene of western America, and interprets the relative sparseness of the Oklahoma material as due to "different physical conditions combined with the much less effective methods of preservation." Although suggesting an Upper Miocene age, he states that "there is no conclusive evidence in existence that such a valley flora may not have continued in this region during the early Pliocene, there being no considerable American Pliocene floras, except that of the Gulf Coast, with which to make comparisons." Within the past decade, Pliocene floras have been described from several localities in western America, and from corresponding habitats in Asia. These floras resemble that from Beaver County in containing fewer species than those of the Miocene and in including plants which are less typical of the humid forests than of the margins of streams in semiarid regions. Like the Beaver County flora, this Pliocene vegetation shows an absence of the redwood element, except in immediate proximity to the Pacific Coast; its oaks are of the live-oak type rather than such broad-leaved species as *Quercus pseudo-lyrata*, which is so abundant in the Upper Miocene; the Asiatic element is largely missing from the Pliocene of western America. Berry's suggestion that the Beaver County type of vegetation may have persisted into the Pliocene seems therefore particularly appropriate in the light of recent studies.

The statistical relationship of the Beaver County flora to those from the Pliocene of western America is less marked than to Upper Miocene vege-

¹ Proc. U. S. Nat. Mus., vol. 54, 629, 1918.

tation, as above discussed. Only 2 species from the Pliocene of California, *Salix coalingsensis* and *Ulmus moorei*, have been recorded at Beaver County. The stratigraphic value of *S. coalingsensis* does not appear to be great, since there are several similar species in the Upper Miocene. Leaves of the *U. moorei* type are restricted to the Pliocene, in western America and China, although a related species, *U. brownellii*, occurs in the Miocene. There are 3 additional species which show close relationships. It is a question whether *Populus prefremontii*¹ from the Pliocene of California is distinct from *P. lamottei* of Oklahoma; they differ only slightly in shape. However, in view of their geographic separation, and because of the fact that living cottonwoods of the two areas are referred to separate species, these species are here recorded as distinct. Most of the leaves of *Platanus paucidentata*,² from the California Pliocene, have longer and more slender lobes and smaller marginal teeth than the leaves of *P. aceroides* from Oklahoma. The variation of leaves of this genus is wide, and certain of the California fossils approach those from our collections. *Fraxinus caudata*³ from the California Pliocene resembles *F. ungeri* in the shape and in the relatively smooth margins of its leaflets. The 5 genera involved in these comparisons, *Fraxinus*, *Platanus*, *Populus*, *Salix* and *Ulmus*, include most of the characteristic plants of the California Pliocene, and the last 3 are especially typical of the Pliocene of Asia as well. The recent discovery of a leaf of *Celtis*, *C. kansana*, in the Orinda formation (Middle Pliocene) of California adds another relationship.

The Esmeralda formation, which is now considered to be of Pliocene age on the basis of its vertebrate fauna,⁴ contains a small flora which has been referred to the Upper Miocene.⁵ From the abundance in it of *Salix*, and of *Typha* and other aquatic types, the senior author has long considered this flora to be of Pliocene age; this possibility has recently been discussed by Dorf.⁶ The Esmeralda flora contains several species which indicate its relationship to the Beaver County flora. *Typha lesquereuxi* is present in both, and although this species has no stratigraphic value in itself, its relative abundance in both floras suggests a topographic condition which appears to have characterized the Pliocene epoch on both sides of the Pacific.⁷ There are leaves which appear to be identical with those of *Salix coalingsensis*, a species characteristic of the California Pliocene; their presence is consistent with the suggestion of an open valley habitat, with small lakes resulting from wind erosion and other causes. The leaflet figured by Berry as *Sapindus lancifolius*⁸ resembles the Oklahoma material in

¹ Dorf, Carnegie Inst. Wash. Pub. No. 412, 77, pl. 7, fig. 4, 1930.

² *Op. cit.* 94.

³ *Op. cit.* 106.

⁴ Stirton, Science, vol. 76, 60, 1932.

⁵ Berry, Proc. U. S. Nat. Mus., vol. 72, 4, 1927.

⁶ Dorf, Carnegie Inst. Wash. Pub. No. 412, 64, 1930.

⁷ Chaney, Svenska Sällskapet för Antropologi och Geografi, Geografiska Annaler 1935, Sven Hedin.

⁸ *Op. cit.* 13, plate 2, fig. 2.

general, although our specimens are more asymmetrical. The writers are in agreement with Berry¹ that the single incomplete specimen from the Esmeralda, referred to *Ficus lacustris*, is not properly assigned to that genus. In the case of such limited material, it is a question whether any generic reference is possible. Berry has named it *Populus lacustris*, which seems reasonable, although it might almost equally well be considered the base of a leaf of *Celtis*; it has the general shape of *Celtis kansana*. *Rhus* (?) *nevadensis* as figured by Knowlton² resembles *Bumelia florissanti*. Small leaves referred by Knowlton to *Cinchonidium* (?) *turneri*,³ are not readily distinguishable from the Oklahoma specimens of *Gymnocladus casei*. Other leaves referred by him to *Quercus argentum*⁴ and *Salix vacciniifolia*⁵ do not show characters either in his descriptions or figures which separate them from *Diospyros pretexana*. All of these latter suggestions are tentative, since the Esmeralda material is poorly preserved and inadequately figured. They are added only to suggest a general similarity between the Esmeralda and Beaver County floras, which resemblance may be more apparent than real.

Summarizing the evidence of the relationship of the Beaver County flora to Pliocene floras of western America, there are 3 species in common, and in addition 5 or more which appear to be related. Several of the Beaver County species are also similar to those from the Pliocene of China, but the details of this relationship will not here be considered. There is a facial resemblance between the Beaver County plants and those from the Pliocene of western America, especially of the interior, which seems much more significant than their statistical relationship. Both lack the humid element which characterizes the Miocene of the Rocky Mountain area and the northern Great Basin; both are made up of species whose modern equivalents occupy a habitat along streams in open grasslands where the rainfall is not sufficient to maintain forests except on the floodplains. In view of the trend toward aridity, which is so well marked in western America during the latter half of the Tertiary period, the age of the Beaver County flora may be said to be Pliocene rather than Miocene. The presence in it of a definite Upper Miocene element is consistent with its geographic position 500 miles to the south of the center of distribution of the Mascall flora during the Upper Miocene. If this flora was shifted southward as a result of late Tertiary reductions in rainfall and temperature, it may be supposed to have reached the southern part of the High Plains during early Pliocene time. In the course of such a migration, the more mesic elements would have been eliminated, leaving a stream-border assemblage such as constitutes the Beaver County flora as we know it.

¹ *Op. cit.* 9.

² U. S. Geol. Surv., 21st Ann. Rept., Pt. 2, 218, pl. 30, fig. 15.

³ *Ibid.* 218, pl. 30, figs. 9-11.

⁴ *Ibid.* 215, pl. 30, fig. 12.

⁵ *Ibid.* 212, pl. 30, figs. 8, 20.

The diatom flora, as studied by Lohman, comprises 37 species, 5 of which are new. Reference to table 2, in which the lists of diatoms from this and the other leaf localities of the High Plains are tabulated, shows that 9 of the Beaver County species, representing 24.3 per cent of the total, occur at the Brown County locality, and that 5 species, representing 13.5 per cent of the total, occur at the Logan County locality. Only 4 species occur at both the Brown and Logan County localities, 2 of which occur also in Beaver County. As Lohman has suggested,¹ the Beaver County flora shows an intermediate relationship between those from Brown County and Logan County and indicates a position closer stratigraphically to the former than to the latter.

The mammalian fauna from beds associated with the leaf-bearing horizon in Beaver County is described by C. J. Hesse elsewhere in this paper. Hesse concludes that this fauna is closely related to that from Valentine, Nebraska, and Clarendon, Texas, which is considered to be of late Lower Pliocene age. The evidence of the vertebrates and diatoms is therefore in agreement with that of the leaves in indicating the Lower Pliocene age of the Beaver County deposits.

THE FLORA FROM LOGAN COUNTY, KANSAS

This flora, much less abundantly represented than that from Oklahoma, can be readily distinguished from it. Not only are there no typical Miocene species included, but there is missing the more humid element of the Beaver County flora, comprising *Cercidiphyllum crenatum*, *Gymnocladus casei*, *Bumelia florissanti* and *Platanus aceroides*. The leaves of certain species occurring at both localities are smaller at the Kansas locality and the whole aspect is one of less humidity, suggesting a younger age.

A statistical comparison shows that only one of the Logan County species regularly occurs in the Miocene, and it is the wide-ranging *Typha lesquereuxi*. *Celtis kansana* and *Ulmus moorei* resemble Miocene species, as above discussed, but the latter species occurs in the Pliocene of California, and its close relative, *U. shansiensis*, is recorded from the Pliocene of China. *Populus lamottei* is the eastern equivalent of *P. prefrementii* from the Pliocene of California. *Salix coalingensis* occurs from the same horizon in California. Three species of the 5 specifically named are recorded elsewhere in the Pliocene, and a fourth is closely related to a Pliocene poplar. The fifth species, *Celtis kansana*, has definitely smaller and thicker leaves than the Miocene species; further, its leaves are smaller and thicker than those representing the same species in the Lower Pliocene of Beaver County. Ten specimens from Logan County average 5.4 cm. in length, while the average of 8 specimens from Beaver County is 8.7 cm. A similar difference in size is noted in the leaves of *Ulmus moorei* from the Logan County locality; they average 2.1 cm. in length as compared with 3.6 cm. for the

¹ Letter of November 22, 1935.

leaves of that species from Beaver County. Leaves of *U. pumila*, now living along dry washes on the borders of the Gobi in central Asia, have similarly small leaves in the more exposed situations. The few specimens of *Populus lamottei* in our collection from Logan County are likewise much smaller than those from Oklahoma. The Pliocene age of the Logan County deposits seems definitely indicated by the flora, and its position in the Middle Pliocene is suggested by its more xeric aspect than the Beaver County flora, which appears to be of Lower Pliocene age.

This age has already been indicated by Elias for the beds which represent the immediate extension of the leaf-bearing deposits to the west into Wallace County.¹ His age determination was based upon the occurrence at this horizon of boraginaceous fruits, *Krynitzkia chanevi* Elias, from a lower subzone which he considers of Middle Pliocene age, and of fruits of the grass *Panicum elegans* Elias, from an upper subzone which he considers of late Middle Pliocene age.² This age reference is in agreement with the determination of the age of these deposits by Stirton, on the basis of fossil vertebrates.³ The presence here of such horses as *Neohipparion* and *Nannippus*, and of the beaver *Dipoides*, is indicative of an age younger than the beds in Beaver County. The evidence of the diatoms is also consistent with the reference of the leaf-bearing deposits of Logan County to Middle Pliocene. Table 2 shows the species which have been recognized by Lohman.

In summary the following conclusions may be suggested regarding the age of the High Plains floras:

(1) The Logan County flora is the youngest, as shown by the xeric character of the plants represented. Its Pliocene age is indicated by the outside occurrence of 3 out of 5 species in beds of that age, as shown in table 3. Of a greater significance in this connection is the Middle Pliocene character of associated mammalian remains. The diatom flora also indicates an age younger than those from the other two localities.

(2) The Beaver County flora is older than that from Logan County, as shown by the more mesic aspect and greater abundance of its floodplain species. Included Miocene species are of the less humid types, representing survivors of a southward migration which eliminated the redwood element so characteristic of Miocene floras to the north. A close facial resemblance is apparent between the flora as a whole and the Pliocene vegetation recorded from western North America and northeastern Asia. The Lower Pliocene age of the Beaver County deposits is indicated by associated mammals. The diatom flora is intermediate between those from Logan and Brown Counties.

(3) The Brown County flora, while too small to offer conclusive evidence of its age, includes species which indicate an age transitional between the

¹ State Geol. Surv. Kansas, Bull. 18, 217, 1931 (in Bull. Univ. Kansas, vol. 32, No. 7).

² *Ibid.* 150.

³ Amer. Jour. Sci., vol. 29, 131, 1935.

Miocene and Pliocene. Associated mammals and diatoms are in agreement with this determination.

PHYSICAL CONDITIONS INDICATED BY THE HIGH PLAINS FLORAS

In his discussion of the flora from Beaver County, Berry has given a brief but accurate description of the habitat occupied by it. Our discussion of the age of the floras from this and other plant-bearing beds in the High Plains has included many references to the physical conditions, since no comprehensive statement of the age of a Tertiary flora can be written without taking the facts of distribution into consideration. The following discussion of the conditions under which these fossil floras lived will therefore be brief, representing a summary of the sequence of climates in later Tertiary time as reflected by the vegetation and the associated mammalian remains.

As previously stated, all of the High Plains floras indicate a climate much less humid than that of the Miocene of the northern Great Basin. The Miocene lake-beds at Florissant likewise indicate a much greater rainfall than that shown by the High Plains floras, but the comparison is less significant since the deposits at Florissant appear to have accumulated at a considerable altitude. The Miocene of the Great Basin appears to have been deposited largely at lower elevations, comparable to those at which the Ogallala formation was deposited. The drier climate of the High Plains is indicated by the absence of the redwood element which is characteristic of most of the floras of the northern Great Basin, an element since eliminated from that region and now confined to the borders of the Pacific from central California to southern Oregon.¹ The climatic implications of the coast redwood, *Sequoia sempervirens*, and its associates are so well defined that the physical conditions in the northern Great Basin during the Miocene, and at other points in the northern hemisphere during this and preceding epochs, can be reconstructed with great accuracy. The habitat of the Lower Miocene, as shown by the Tertiary redwood, *S. langsdorffii*, and associated species,² has been discussed by Chaney.³ Studies of the later Miocene floras by Chaney and his associates⁴ have shown some reduction in dominance of the redwood association, but its wide-spread occurrence in the western United States at this date is also a matter of general record. It is

¹ A modified redwood forest is also living today at middle elevations in the Sierra Nevada, but this is less like the Miocene redwood assemblage than the forest of the California Coast.

² *Alnus carpinoides* (alder), *Quercus consimilis* (tan-oak), *Umbellularia oregonensis* (laurel), *Acer* spp. (maple) are the more characteristic fossil species.

³ Carnegie Inst. Wash. Pub. No. 349, 1925.

⁴ Carnegie Inst. Wash. Pub. No. 349, 1925; MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 1933; Oliver, Carnegie Inst. Wash. Pub. No. 455, 1934; LaMotte, Carnegie Inst. Wash. Pub. No. 455, 1936.

not present, however, in deposits of Pliocene age except in the case of those adjacent to the present Redwood Belt along the Pacific Coast.¹ This has been interpreted as due to progressive desiccation, with associated extremes of temperature, under which conditions *Sequoia* was eliminated and other conifers, notably *Pinus*, have taken its place. The absence of the redwood element from the High Plains floras is therefore consistent, as above indicated, with their reference to latest Miocene and post-Miocene time. Only the hardier type of plants has survived into the Pliocene, and with a single exception, *Cercidiphyllum crenatum*, whose living descendants are restricted to eastern Asia, all of these have continued to live in the High Plains area. Their range, however, has been restricted since the close of the Tertiary period, so that living representatives of several genera no longer exist in the areas where the fossils occur.

It seems probable that even in the Miocene, when the annual precipitation in the northern Great Basin was between 40 and 50 inches at the beginning, and approximately 30 inches near the close of the epoch, the humidity in the High Plains area was much less. At this time the Cascade Range was only in the process of being built up and did not serve as an effective climatic barrier to the Great Basin area, as has been the case since the Pliocene. But the Rocky Mountains, lying to the west and windward of the High Plains, may be supposed to have had greatly reduced precipitation in that region during the Miocene, as they do today. The general scarcity of middle Tertiary floras in the area east of the Rockies is well known and has been interpreted as due to these climatic relations. Only in the mountains themselves, where the Missoula and Florissant lake-deposits were accumulating under conditions of humid and relatively equable climate, is there a record of the *Sequoia* forest, and even there it was present in considerably modified form. The lake beds from Creede, at a probably higher Tertiary elevation in southwestern Colorado,² contain no *Sequoia*, its place being taken by several species of *Pinus* and *Abies* which make up a dominant element in the flora. It may therefore be supposed that the Miocene vegetation of the High Plains was of a more xeric type than those from similar elevations in the Great Basin. The floras as known, and the associated mammalian remains, point toward climatic conditions which favored the development of broad grasslands, with forests restricted to the stream borders.

Only one of the High Plains floras above discussed is considered to be of Miocene age—that from Brown County, Nebraska; and even it appears to lie on the border between the Miocene and Pliocene. In addition there is the fragmentary material of *Salix* from Morrill County, Nebraska, which is considered to be of lower Miocene age. It is significant that the most abundant species of the Brown County flora are *Typha lesquereuxi* and

¹ Dorf, Carnegie Inst. Wash. Pub. No. 412, 73, 1930.

² Knowlton, U.S.G.S., Prof. Paper 131, 1923.

Platanus aceroides. The presence of *Typha*, and of the fragmentary remains referred to *Cyperacites*, indicates that lake basins formed a characteristic topographic feature. While some of these may have originated on floodplains, the possibility must be considered that they were formed by wind deflation, as has been suggested in the case of somewhat similar deposits in Turkestan.¹ *Platanus* is a genus which is in most cases confined to stream borders. In more humid areas of the United States, the living *P. occidentalis* may be distributed over broad floodplains; in the more arid western portion of its range, it is confined to stream borders, as is the case with the western species, *P. racemosa*. The latter situation seems to approximate the late Miocene occurrence of *P. aceroides* in the High Plains. For while the closely related or identical fossil species, *P. dissecta* of the Great Basin and Pacific Coast, is associated with *Sequoia*, *Alnus*, *Umbellularia* and other mesic plants, the High Plains sycamore leaves occur only with those of *Salix* and *Fraxinus*, both of which genera are also characteristic stream border types in semiarid plains at the present time. The presence of grasslands is more than implied, since Elias has found the seeds of *Stipidium* γ in deposits which he considers to be of the same age at several localities in northern Nebraska.

Farther south, climatic conditions may be supposed to have been better suited for tree growth. Due perhaps to rainfall derived from the Gulf of Mexico, or less effectively shut off by the mountain barrier to the west, the floras along the southern front of the Rockies, as early as Eocene time, were of a more humid type than those to the north. The flora from Beaver County, Oklahoma, is likewise indicative of a climate more moist than that indicated by the Nebraska fossils. No remains of grass seeds have as yet been found to indicate the presence of grasslands, but the presence of the same horses which are associated with the grass floras at Valentine leads to the conclusion that grasslands were well developed. The vegetation of the stream borders was, however, of a much more humid type than at Brown County, Nebraska. Living at a slightly later time, near the end of the lower Pliocene, when the trend of climatic change may be expected to have brought increasingly drier conditions to western America, the Beaver County flora is relatively rich in floodplain trees. While it contains only one species, *Cercidiphyllum crenatum*, which may be considered to have been a typical member of the humid redwood forest to the north and west, this Oklahoma flora includes *Acer* (box-elder), *Bumelia*, *Celtis*, *Diospyros*, *Fraxinus*, *Gymnocladus*, *Platanus*, *Populus* (cottonwood), *Salix* and *Ulmus*, most of which genera are represented in the modern vegetation along the eastern border of the High Plains. Since they make up a floodplain assemblage definitely more mesic than that now found in western Oklahoma, the climatic change since the lower Pliocene can be measured by their subsequent eastward restriction. The distribution of the modern equivalents of

¹ Chaney, Svenska Sällskapet för Antropologi och Geografi, Geografiska Annaler 1935, Sven Hedin, 85.

the Beaver County species is shown in table 4, on the basis of data supplied by J. C. Shirley. Several species extend farther west into New Mexico and Texas.

TABLE 4—Distribution of modern floodplain species corresponding to fossil species from Beaver County.

Fossil Species	Modern Species	Western limits in Oklahoma	
		County	Distance in miles east of fossil locality
<i>Acer negundoides</i>	<i>Acer negundo</i>	Caddo	110
<i>Bumelia florissanti</i>	<i>Bumelia lanuginosa</i>	Roger Mills	35
<i>Celtis kansana</i>	<i>Celtis reticulata</i>	Roger Mills	35
<i>Diospyros pretexana</i>	<i>Diospyros virginiana</i> ¹	Greer	45
<i>Fraxinus ungeri</i>	<i>Fraxinus americana</i>	Comanche	105
<i>Gymnocladus casei</i>	<i>Gymnocladus dioicus</i>	Roger Mills	35
<i>Platanus aceroides</i>	<i>Platanus occidentalis</i>	Kay	180
<i>Populus lamottei</i>	} <i>Populus sargentii</i> ² <i>Populus deltoides</i>	Comanche	105
		Roger Mills	35
<i>Salix coalingensis</i>	<i>Salix nigra</i> ³	Roger Mills	35
<i>Sapindus oklahomensis</i>	<i>Sapindus drummondi</i>	Cimarron	0
<i>Ulmus moorei</i>	<i>Ulmus fulva</i> ⁴	Comanche	105

¹ Distribution of this species is here given rather than that of the more closely related *D. texana*, since the latter does not occur in Oklahoma. It ranges into southwestern Texas and adjacent Mexico.

² Data are given for two living species of poplar, since the fossil specimens appear to be equally related to both.

³ *Salix lasiolepis*, which represents the closest living equivalent of the fossil species, is confined to California and Arizona. A common Oklahoma species is here substituted for it.

⁴ Distribution of this species is here given rather than that of the more closely related *U. crassifolia*, since the latter does not occur in Oklahoma. It ranges into southwestern Texas and adjacent Mexico.

Of the modern related species here listed, only *Sapindus drummondi* extends as far west as Beaver County. With few exceptions, the remainder are most abundant in the eastern half of the state. *Platanus occidentalis*, whose equivalent fossil species was the most abundant Pliocene tree, judging from the record, does not now occur in the western half of the state; where observed from Oklahoma City eastward by Chaney, it has nowhere held the dominant position in the floodplain flora that it may be assumed to have occupied during the Pliocene. The rainfall in Beaver County at present is 19.98 inches a year, some 15 inches less than that in the eastern part of the state where the modern vegetation is similar to that of the Pliocene. This may be considered to represent the approximate reduction in rainfall in Beaver County since that epoch.

During recent field studies of the modern vegetation in eastern Oklahoma and adjacent Kansas, floodplain assemblages have been noted at several localities which approximate the Beaver County fossil flora in composition. Six miles south of Medford, in north central Oklahoma, the dominant species, on the floodplain in a small open valley, are *Bumelia lanuginosa*, *Celtis reticulata*, *Fraxinus americana*, *Populus deltoides*, *Salix nigra*, *Ulmus fulva*, and *Gleditsia triacanthos*. All but the last of these are represented by fossil equivalents at the Beaver County locality. In addition, *Sapindus drummondii* is present on the borders, and *Tilia nuda* and *Prunus* sp. occur in small numbers. Generic representatives of 7 of the 12 Beaver County fossils are here present, those absent being *Acer negundo*, *Diospyros*, *Gymnocladus*, *Platanus* and *Typha* for which there is no suitable environment. All of these are common at present in the more humid portion of the state to the east. While the Medford habitat may be considered to resemble that in Beaver County during the Pliocene, it appears to be somewhat drier. The fact that the stream was not flowing in June 1935, after several dry years, is an indication of a relatively low precipitation. No figures are available for this immediate region, but at Enid, 25 miles almost due south, the annual rainfall is 30.44 inches, as compared to 19.98 inches at the town of Beaver, near the fossil locality.

The valley of the Canadian River, south of Oklahoma City, is much larger than that near Medford, and the floodplain vegetation is richer in species and more luxuriant. This region lies 100 miles south of Medford, and slightly to the east. *Fraxinus pennsylvanica*, *Juglans* sp., *Populus deltoides*, *Salix nigra* and *Ulmus americana* are the dominant trees here, with the following species, or genera, also represented: *Bumelia lanuginosa*, *Carya* sp., *Celtis* sp., *Cercis canadensis*, *Cornus* sp., *Diospyros virginiana*, *Gymnocladus dioica*, *Ilex* sp., *Juniperus* sp., *Morus rubra*, *Quercus muhlenbergii*, *Rhus glabra*, *Rhus toxicodendron*, *Smilax* sp., *Tilia* sp. and *Vitis* sp. On the more open slopes of adjacent ravines, *Sapindus drummondii* is common. In the valleys of a small tributary, *Celtis* sp., *Diospyros virginiana*, *Populus deltoides*, *Salix nigra*, and a species of *Ulmus* with small leaves, probably *U. alata*, are dominant, with *Bumelia lanuginosa*, *Prunus demissa* and *Gleditsia triacanthos* common on the borders. These lists include 9 of the 11 genera of the fossil flora from Beaver County, and the resemblance between the living and Pliocene plant assemblages must be considered to be close. The absence of *Platanus occidentalis* from the Canadian River forest, and the presence of *Quercus muhlenbergii*, represent important differences. *Platanus* is not a conspicuous member of the floodplain forest as far west as central Oklahoma; as observed by Chaney, it reaches its best development, both in size and numbers, in a more northerly situation and to the east, in the Mississippi basin. The dominance of its Tertiary equivalent, *P. aceroides*, at the Beaver County locality, suggests a climate somewhat more humid than that at the Canadian River locality today, where the

annual precipitation averages 31.15 inches. The absence of *Quercus muhlenbergii* from the fossil record of Beaver County is difficult to explain. As has been suggested elsewhere in this paper, it may be due to the fact that in Pliocene time this and other broad-leaved species of oak had not extended their range into western Oklahoma, in which region *Q. muhlenbergii* does not occur at the present time.

Twenty-five miles east of Medford and slightly to the south, near Tonkawa, Oklahoma, the South Fork of the Arkansas River is bordered by a forest containing trees of *Platanus occidentalis* up to 75 feet in height, together with *Acer negundo*, *Carya* sp., *Celtis* sp., *Cercis canadensis*, *Cornus* sp., *Fraxinus pennsylvanica*, *Juglans* sp., *Morus rubra*, *Populus deltoides*, *Quercus macrocarpa* (1 small tree), *Salix nigra*, *Smilax* sp., and *Ulmus americana*. Still farther east in the valley of the Arkansas River, many of these same species were noted, together with large trees of *Gymnocladus dioica*. *Bumelia lanuginosa* and *Sapindus drummondi* occur at nearby points. Altogether, 10 of the 11 tree species of the Beaver County Pliocene have been recorded in north central Oklahoma. The precipitation in this area, as recorded at Blackwell, is 32.70 inches a year. Forty miles north and slightly west, near Wellington, Kansas, most of the Beaver County fossil genera are represented in the valley forest, but *Platanus* is missing. The precipitation here is slightly less than at the localities to the south where it is present. The abundance of leaves of *Platanus* in the fossil flora, and its absence or comparative scarcity at most of the localities in central Oklahoma, suggest that the rainfall in Beaver County during the early part of the Pliocene may have been at least as high as at Blackwell. The average precipitation in the eastern part of Oklahoma, where *Platanus occidentalis* and the other living representatives of the Beaver County are most abundant, is nearly 42 inches a year.

The presence of *Gymnocladus casei* and *Bumelia florissanti* in the Pliocene deposits of Beaver County, and the comparatively common occurrence of *Diospyros pretexana*, suggest that the temperature was somewhat higher there than at points to the north in the Great Basin, where many of the Beaver County species have previously been recorded. This is consistent with the difference in latitude of the two areas and with their present difference in mean annual temperature. At the nearest available point to Beaver, the town of Hooker, lying some 25 miles to the west and 800 feet higher, the mean annual temperature is 55.7°. This is 4.3° higher than that at Dayville, Oregon, which has approximately the same elevation as the fossil locality in Beaver County. Dayville is situated in the John Day Basin, in the midst of the area in which the Mascall flora has been found. This flora, as elsewhere discussed, contains many of the fossil species which occur in Oklahoma, but in addition includes others which now require a more humid climate. The late Tertiary difference in temperature between Oregon and Oklahoma may be assumed to have been of the order of that of

today. The precipitation required by the Mascall flora has been estimated at about 30 inches a year,¹ with a reduction to 25 inches to the south in Nevada.² It may be assumed that the somewhat higher rainfall at the Oklahoma locality was more than offset by the warmer temperature, so that the climate was actually less humid than in Oregon. In any event the vegetation was definitely more mesic in Oregon than that of somewhat later age in Oklahoma.

The occurrence of scattered plant remains at Clarendon, Texas, in beds considered, from their mammalian remains, to represent the same age as those of Beaver County, adds corroborative evidence of the latitudinal variations in climate in western America during late Tertiary time. The Clarendon material, now being studied by Mason, includes wood of *Fraxinus*, a seed of *Arctostaphylos*, and several seeds of palm. While no general conclusions as to physical conditions can be reached from so small a collection, the climate appears to have been warmer and less humid than that in Beaver County, 135 miles to the north.

Summarizing the evidence of the Beaver County flora with regard to physical conditions, the following suggestions may be made:

(1) There was sufficient rainfall to support a floodplain forest like that in central to eastern Oklahoma, 180 or more miles to the east, where modern equivalents of all of the arboreal species are now living. The annual precipitation there is in excess of 30 inches, which may be considered to represent the approximate minimum in Beaver County during the Lower Pliocene. A reduction in rainfall of 10 or more inches a year appears to have occurred in this region since that time.

(2) The absence of evergreen oaks, which are so characteristic of the later Miocene and Pliocene floras of the Pacific Coast, may be interpreted as indicating that the rainfall was concentrated during the warmer months, as is the case in Oklahoma at the present time. This is consistent with the presence of the Rocky Mountains to the windward of Beaver County during the Pliocene, which gave this region a continental type of climate.

(3) The temperature is considered to have been somewhat warmer than in western Oklahoma today, and considerably warmer than that in the northern Great Basin, where a somewhat similar assemblage of plants is known to have lived during the Miocene.

The more xeric aspect of the Logan County flora, as compared with that from Beaver County, is consistent with both its somewhat younger age and with its position 150 miles to the northwest. As elsewhere mentioned, *Platanus aceroides* does not occur there, and such other relatively mesic genera as *Gymnocladus*, *Acer (negundo)*, and *Cercidiphyllum*, and southern genera such as *Bumelia*, *Diospyros*, and *Sapindus* are also absent. All of

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, 47, 1925.

² LaMotte, Carnegie Inst. Wash. Pub. No. 455, V, 1936.

the 4 tree species, *Celtis kansana*, *Populus lamottei*, *Salix coalingensis* and *Ulmus moorei*, have leaves averaging smaller than those of these species in the Lower Pliocene of Oklahoma. This is particularly marked in the case of *Celtis kansana*, as may be seen by a comparison of the Logan County and Beaver County leaves figured on Plate 5. The general extent of grasslands on the uplands is indicated by the occurrence of seeds of grass and associated boraginaceous herbs, as reported by Elias from Middle Pliocene deposits over a wide area.¹ Lohman has pointed out that the abundance of the diatom, *Amphiprora alata*, in the leaf-bearing layer suggests rather saline water.² It may be concluded that habitat conditions approaching those in the region at the present time characterized western Kansas during the Middle Pliocene. The most westerly elm, *Ulmus americana*, does not range west of central Kansas today. The annual precipitation there averages under 25 inches, as compared with an average of nearly 20 inches in Logan County. It should be mentioned that *Ulmus parvifolia* of Asia, which in size and other characters is more closely similar to the Pliocene species than are any living American elms, lives today in areas of similarly low rainfall. The composition of the Logan County flora seems therefore to point toward a Middle Pliocene climate with at least 5 inches less rainfall than that in Oklahoma during the Lower Pliocene, and with approximately 5 inches more rainfall than in the region today.

The evidence of the High Plains floras regarding physical conditions during later Tertiary time may be summarized as follows:

(1) All of the floras are less mesic than those of the Miocene of the northern Great Basin, with which they show a general resemblance. This is due in part to their position in the interior of the continent, on the eastern side of the Rocky Mountain barrier. It is due also to their somewhat younger age; the trend toward aridity, which is especially apparent in western America during later Tertiary time, had resulted in a reduction of rainfall, at the end of the Miocene and during the Pliocene, to a point where the more humid element of the Miocene flora could no longer occupy this region. The survivors were representatives of more hardy genera which have continued down to the present, fringing the streams in areas of moderate rainfall, where grasslands occupy the uplands.

(2) The High Plains floras show differences resulting from their geographic and stratigraphic position. The oldest, from western Nebraska, is considered to occur in deposits of an age transitional between the Upper Miocene and the Lower Pliocene. It lies 350 miles to the south and about 800 miles to the east of the area in Oregon which was occupied by the related Mascall flora during the Upper Miocene. During the restriction of the

¹State Geol. Surv. Kansas, Contributions to Paleontology 1, 333-367, 1932 (in Bull. Univ. Kansas, vol. 33, No. 10, as Univ. Kansas Sci. Bull., vol. 20, No. 20).

²Written communication of September 3, 1935.

Mascall southward, there were eliminated those genera with more humid requirements, of which *Sequoia* and its associates are the most significant. This Nebraska flora lies approximately 350 miles to the north and 150 miles to the west of the area in which the Beaver County flora of Oklahoma is found. Its age is considered to be late Lower Pliocene, and it represents a floodplain assemblage more humid in character than that from western Nebraska. This is not inconsistent with the idea of a Tertiary trend toward aridity, since its geographic position is considerably to the south and east, a gap which may be considered to represent the southwestward restriction of the Miocene flora during the early Pliocene. It has been further restricted in post Lower Pliocene time, so that the equivalent living species occupy an area 180 miles or more to the east, in eastern Kansas, Nebraska, and Oklahoma. The youngest of the High Plains floras, from western Kansas, is referred to the Middle Pliocene. It comprises a group of genera from which most of the more mesic Beaver County genera have been eliminated, in keeping with its younger age and its position 150 miles to the north and slightly west. A valley assemblage resembling it ranges into the High Plains at the present time, but not as far west as Logan County in which the fossils occur. There appears to have been a reduction of approximately 5 inches in annual rainfall since Middle Pliocene time.

(3) In addition to the progressive elimination of those genera which had higher moisture requirements, there is apparent in the High Plains floras the appearance of new generic elements. These may be supposed to have been developing toward the east or the south, since they have not been recorded in Tertiary floras west of the Rocky Mountains, and since their modern species are now confined to the eastern United States on this continent. *Gymnocladus* and *Bumelia*, examples of such genera, are represented by fossil species in the Lower Pliocene of Beaver County. *Hamamelis*, from the transitional beds at the top of the Upper Miocene in north central Nebraska, has been previously unrecorded in the Tertiary of North America, although several species of *Hamamelites* from the Cretaceous and Eocene east of the Rockies have been considered to be of a related type. The occurrence of *Arctostaphylos* in the Lower Pliocene of Texas represents the earliest appearance of a genus which by Middle Pliocene time was becoming established in California. It is a conspicuous element in the Pleistocene floras, and is wide-spread at the present time. This genus is considered by Mason to have come up from Mexico.¹ As above mentioned, the absence of broad-leaved oaks from the High Plains Tertiary is noteworthy in view of their abundance in the related modern vegetation to the east. It may be supposed that *Quercus* moved into the region more slowly than *Gymnocladus*, *Bumelia* and other new genera, arriving in post Middle Pliocene time.

(4) The addition of certain genera and the elimination of others, in the course of the development of vegetation in the High Plains during later

¹ Mason, Carnegie Inst. Wash. Pub. No. 415, 173, 1934.

Tertiary time, have an important stratigraphic as well as floristic significance. These changes in floral composition illustrate the effects of migration for a distance of about 1000 miles, over a length of time involving most of the Upper Miocene, and the Lower and Middle Pliocene. During these epochs the precipitation in western America was being steadily diminished, due in large part to orogenic and volcanic activity which created additional climatic barriers. As the northern margin of the Miocene type of vegetation was shifted southward, due to lessened rainfall, the plant assemblage was modified to such an extent that it may readily be distinguished from the ancestral Mascall flora to the north. Although certain genera and even species continued from the Miocene into the Pliocene, there was a sufficient loss of some and gain of others to give the latest Miocene and Pliocene floras of the High Plains a recognizable stratigraphic character. Continuing reduction of rainfall since the Middle Pliocene has resulted in a further shifting of the modern equivalents of these later Tertiary floras to their present ranges in eastern Nebraska, Kansas and Oklahoma, and in additional changes in composition of the modern vegetation.

The evidence of the vertebrate fauna from Beaver County, as presented below by Hesse, is in full accord with the climatic conclusions derived from a study of the fossil plants. This fauna is made up predominantly of grazing types which definitely indicate the presence of extensive grasslands in Oklahoma during the Pliocene. A subordinate element of savanna and woodland types may be considered to have inhabited the valleys, to which trees were restricted. The presence of the bones of upland mammals in the stream deposits is consistent with the habits of modern inhabitants of the plains, which go down to the streams for water.

SYSTEMATIC DESCRIPTIONS

Subclass MONOCOTYLEDONÆ

ORDER PANDANALES

Family TYPHACEÆ

Genus TYPHA L.

Typha lesquereuxi Cockerell

Typha lesquereuxi Ckll., Cockerell, Bull. Amer. Mus. Nat. Hist., vol. 24, 79, pl. 10, fig. 46, 1908; Knowlton, U. S. Nat. Mus., Proc., vol. 51, 251, 1916.

Typha latissima Al. Braun, Lesquereux, U. S. Geol. Surv. Terr. Rept., vol. 8, 141, pl. 23, figs. 4, 4a, 1883.

This species is present at most of the localities, but is sparsely represented in all of these except in Brown County, Nebraska. Here it comprises over half of the total of specimens collected and may be considered to have constituted an important element of the vegetation. There is no basis for determining that certain smaller specimens may not be referable to other aquatic monocotyledonous genera, but the more common larger specimens seem definitely assignable to this genus and species.

Family SPARGANIACEÆ

Genus CAULINITES Brongniart

Caulinites sp.

Fragmentary remains resembling the leaves of *Sparganium* occur at several localities, and may be referable to the same type of plant as the specimens placed in this form genus by Berry.¹ They are of about the size of leaves of the modern *S. simplex* Hudson, whose Miocene equivalent has been recorded by LaMotte at 49 Camp, Nevada, on the basis of a well-preserved fruit.² Such a relationship was evidently suspected by Lesquereux in his description of *Caulinites sparganioides*, and his figure 11, showing a leaf fragment, is not unlike our material.³

ORDER GLUMIFLORÆ

Family CYPERACEÆ

Genus CYPERACITES Schimper

Cyperacites sp.

(Plate 4, fig. 2)

In addition to leaf fragments, which are apparently referable to the sedge family, and which are sparingly represented at all of the localities, there are several fruits which resemble those of such genera as *Cyperus* or *Carex*. One of these is figured on Plate 4. The systematic position of this material is too uncertain to warrant its description as a fossil species.

The sedge-covered borders of many lakes, especially in semiarid regions of western America and central Asia, suggest the habitat occupied by the plants from which these specimens were derived.

Collection—U. S. Nat. Mus., Plesiotype, No. 39333.

Subclass DICOTYLEDONÆ

ORDER SALICALES

Family SALICACEÆ

Genus POPULUS L.

Populus lamottei n. sp.

(Plate 4, figs. 4, 5)

Description—Leaves deltoid to orbicular, rounded or narrowed to a short point at the apex, the base broadly rounded bluntly cuneate at the point of attachment; length 2.2 to 5.5 cm., width 2.7 to 7 cm., with the leaves only rarely longer than wide; petiole slender, flattened near point of attachment to leaf, incomplete or missing in all specimens; midrib slender, tapered, curving; secondaries alternate, with two pairs closely spaced near the base, where they branch out at high angles, spreading out toward the margin and curving apically to extend parallel with the more distal secondaries which leave the midrib at an angle averaging 40°; those in distal part of blade curving more abruptly apically on approaching margin where they

¹ U. S. Nat. Mus., Proc., vol. 54, 629, 1918.

² Carnegie Inst. Wash. Pub. No. 455, V, 1935.

³ U. S. Geol. Surv. Terr., Rept., vol. 7, 99, pl. 14, 1878.

run into teeth; 3 to 4 pairs of subsecondaries on mesial basal pair of secondaries; tertiaries trend at high angles to secondaries commonly obscured by nervilles which form reticulate background; margin irregularly toothed, round to serrate broad at base and terminating in sharp tips usually recurved apically; texture firm.

This species is named in honor of Dr. R. S. LaMotte, who has suggested its relationship to living poplars of the cottonwood type rather than to those of the aspen type. There are several living cottonwoods whose leaves bear a definite resemblance to our fossil specimens. Of these may be mentioned *Populus sargentii*, which ranges along the east front of the Rockies and eastward into the High Plains; *P. deltoides*, an eastern species which extends into the High Plains; and *P. fremontii* which extends from west central California into Lower California. Geographically intermediate species such as *P. arizonica*, *P. texana* and *P. wislizenii* also have similar leaves. It seems possible that during the Tertiary, not all of these living species may have been distinct, either in leaf characters or in range. In any event, the fossil species, *P. lamottei*, has leaves which fall within the present limits of variation of several of them. In view of its occurrence in northwestern Oklahoma and northwestern Kansas, *P. lamottei* may probably best be considered to represent the Tertiary equivalent of *P. deltoides* or *P. sargentii*, whose modern ranges include the western part of both of these states.

From several Pliocene localities in California, Dorf has described leaves of a poplar related to *P. fremontii*, to which he has applied the name *P. prefremontii*.¹ A close relationship is apparent between this species and *P. lamottei*; with more material for comparison, and with fossil occurrences in geographically connecting areas, our fossil species from Oklahoma might be found to be specifically inseparable from *P. prefremontii* of California. Minor differences in the shape, nervation and margin of the two species seem sufficient to justify their being considered distinct for the present.

P. lindgreni, which is widely distributed in the Miocene of the northern Great Basin, is less deltoid in shape, with a base more cordate; its modern relationships lie with the aspen, *P. tremuloides*, rather than with the various species of cottonwood. It is a question whether our material is specifically distinct from *P. richardsoni* Heer, as recorded by Lesquereux from the Upper Miocene at Elko, Nevada.² It is surely not the same as that originally described by Heer in his Arctic floras. *P. heliadum* and *P. attenuatum*, as figured by Heer³ from Oeningen, have margins and shapes generally similar to the leaves of our specimens, but can not be considered conspecific. Certain leaves of *P. hedini*⁴ from the Pliocene of Turkestan have a form suggestive of *P. lamottei*, but the margins of the Turkestan species have larger and fewer teeth.

Wood from the uppermost Miocene in Cherry County, Nebraska, is referred by Daugherty to this genus, which seems to have been widely distributed over the High Plains during late Tertiary time.

Occurrence—Beaver County, Oklahoma, Loc. P-44; Logan County, Kansas, Loc. P-43.

Collection—U. S. Nat. Mus., Cotypes, Nos. 39334, 39335.

¹ Dorf, Carnegie Inst. Wash. Pub. No. 412, 77, 1930.

² Rept. U. S. Geol. Surv. Terr., vol. 7, 177, pl. 22, figs. 10-12, 1878.

³ Fl. tert. Helv., vol. 2, pl. 57, figs. 4, 5; pl. 57, figs. 10, 12, 1856.

⁴ Chaney, Svenska Sällskapet för Antropologi och Geografi, Geografiska Annaler 1935. Sven Hedin, 100-101, pl. 3, figs. 1-4.

Genus *SALIX* L.*Salix coalingsensis* Dorf

(Plate 4, figs. 1, 3, 6)

Salix coalingsensis Dorf, Carnegie Inst. Wash. Pub. No. 412, 78, pl. 7, figs. 5-7; pl. 8, figs. 1, 2, 1930.

The leaves of modern willows are so variable and in some cases so closely approach those of other living species, that it may be difficult to distinguish certain forms on the basis of their leaves alone. The palaeobotanist, whose material of this genus is mostly leaves, finds similar difficulty in distinguishing fossil species and in relating them to their living equivalents. There is no question that the species of Tertiary *Salix* have been multiplied to an extent which obscures not only their modern relationships but their stratigraphic value as well.

In the case of the leaves from the High Plains floras, the absence or rarity of marginal teeth serves as a character relating them to *S. coalingsensis* from the Pliocene of California. Our fossil leaves vary greatly in size, and to some extent in shape, but they are consistently entire-margined or nearly entire; this type of margin is comparatively rare, both in Tertiary and modern willows, and serves to distinguish them.

Salix coalingsensis is one of the most widely distributed species of the California Pliocene. It is considered to represent the Tertiary equivalent of *S. lasiolepis* Benth., a modern species largely confined to the Pacific Coast of California and Lower California. Its present distribution shows a significant occurrence in southeastern Arizona and adjacent New Mexico, with no intermediate stations. This distribution is wholly consistent with the wider distribution of the Tertiary equivalent, *S. coalingsensis*, both in California and in Oklahoma.

Without attempting to revise the fossil species of willow, the suggestion may be made that the Tertiary range of its close relatives was also extensive to the north during the Miocene. Similar leaves have been noted as *S. elongata* O. Weber, from the Upper Miocene at Elko, Nevada, from the Latah formation at Coeur d'Alene, Idaho, and doubtfully from Yellowstone Park; another almost entire-margined species is *S. remotidens* Kn. from the Latah formation at Spokane, Washington, whose age is apparently Upper Miocene; *S. dayana* Kn., from the Latah formation of Idaho and the Mascall of the John Day Basin, Oregon, has a shape similar to that of some of our leaves and is entire-margined; *S. californica* Lesq., from the Miocene at Table Mountain, California, and from the Lower Miocene of the Crooked River Basin, Oregon, is likewise related. *S. vacciniifolia* Kn., from the Pliocene Esmeralda beds of Nevada, has leaves of the same type, though not all of them appear to be those of willow. Several small leaves designated as *Salix* sp. are also similar to our material. Further studies may show that several or all of these species are identical. For the present, the specific identity of our Oklahoma specimens with *S. coalingsensis* from the Pliocene of California is all that need be established.

While the leaves of *S. coalingsensis* are more similar to those of *S. lasiolepis* than to other modern American species of willow, it may be noted that certain of our fossil leaves also resemble those of the living *S. laevigata* Bebb. This species has an obscurely toothed margin, but is otherwise similar to *S. lasiolepis* and *S. coalingsensis*. Some of the California specimens of *S. coalingsensis* are likewise obscurely toothed, and Dorf has mentioned¹

¹ Dorf, Carnegie Inst. Wash. Pub. No. 412, 78, 1930.

their resemblance to *S. lævigata*. This modern species, while mostly confined to California, occurs also in Nevada, Utah and Arizona. It is possible that *S. coalingensis* may represent the Tertiary equivalent of both *S. lasiolepis* and *S. lævigata*, and perhaps of other living species which have become differentiated since the Pliocene epoch.

All localities.

Collection—U. S. Nat. Mus., Plesiotypes, Nos. 39336, 39337, 39338.

ORDER URTICALES

Family ULMACEÆ

Genus *CELTIS* Tourn.

Celtis kansana n. sp.

(Plate 5, figs. 1-5)

Description—Leaves ovate to deltoid, apex acuminate or bluntly tapering, base subtruncate, obliquely asymmetrical; length 4.2 to 11.5 cm. (estimated), width 2.2 to 5.2 cm.; petiole incompletely preserved, strong at attachment to leaf, somewhat curved; midrib firm, tapering, curved; a pair of basal secondaries diverge at angles of 25° to 50° from midrib immediately within blade at petiole attachment, producing in some specimens a pseudo-palmate appearance; 4 to 5 pairs of abaxial secondaries diverge from basal secondaries; remaining secondaries alternate to subopposite, diverging from midrib at 30° to 50° angles, curving apically, forming broad loops with adjacent secondaries or loops into which marginal tertiaries enter; tertiaries, where preserved, conspicuous, some approaching subsecondaries in caliber, forming large, well-defined irregular polygons; margin dentate-serrate to crenate; texture firm. Fragment of endocarp globular, 4 mm. in diameter, surface with obscure lines.

This species is abundant at the Beaver County, Oklahoma, and the Wallace County, Kansas, localities. A general difference may be noted between the leaves at the two localities; those from Oklahoma average larger in size, are thinner, and are more finely serrate than those from Kansas. However, their reference to a single fossil species appears to be justified because of the occurrence of a few of the small, subcoriaceous leaves at Beaver Creek. Moreover, this difference in leaf character at the two localities is no greater than may be observed in the leaves of the modern related species, *C. reticulata* Torr. A certain amount of confusion appears to have arisen as to the distinctions between several of the living species of *Celtis* in America. Sargent has differentiated them on the basis of leaf and fruit characters,¹ but these distinctions do not seem to have been used by all of the systematic botanists who have identified specimens of this genus which are found in American herbaria. Perhaps the most convenient basis, and one also emphasized by Sargent in his descriptions of American species, is their geographic distribution.

A study of the leaves of *C. reticulata* in the herbaria of the New York Botanical Garden and the University of California shows that all of the leaf variations represented in our fossil specimens occur also in the leaves of this living species. The larger and thinner leaves come from trees which occupy stream borders and moist floodplains, while small, thick leaves characterize the trees of dry slopes. *C. reticulata* is now recorded from western Texas and Oklahoma into New Mexico and Arizona.

¹ *Manual of the Trees of North America*, pp. 318-319.

C. kansana is closely related to *C. obliquifolia* from the Lower Miocene of Oregon. It differs somewhat in the shape of the base, in the details of basal nervation, and in having an entire margin. None of the specimens from Oregon are as thick as those from the Kansas locality, which is consistent with the occurrence of *C. obliquifolia* on the borders of a red-wood forest.¹ In view of these differences, and of the wide geographic distance separating the two fossil occurrences, their relations are best represented by designating them as distinct species.

The larger of the two specimens described by Lesquereux as leaflets of *Fraxinus heeri*, from the Florissant beds,² appears to represent a small leaf of *Celtis kansana*. On the other hand, the specimens recorded as *C. mccoshii* by the same author from Florissant³ are clearly unrelated to *C. kansana*; both in shape and nervation they differ from living leaves of hackberry, and do not appear to be correctly referred to that genus.

Occurrence—Beaver County, Oklahoma, Loc. P-42; Logan County, Kansas, Loc. P-43.

Collection—U. S. Nat. Mus., Cotypes, Nos. 39339-39343.

ORDER URTICALES

Family ULMACEÆ

Genus ULMUS L.

Ulmus moorei n. sp.

(Plate 6, figs. 1-5)

Ulmus brownellii Lesq., Dorf, Carnegie Inst. Wash. Pub. No. 412, 92, pl. 10, figs. 1, 2, 3, 10, 1930.

Description—Leaves ovate to orbicular, apex varying from blunt to acuminate, base broad cuneate or slightly cordate, nearly symmetrical; length 1.2 to 3.5 cm., width 1.1 to 2.2 cm.; petiole not preserved; midrib slightly curving, tapered; 7 to 8 pairs of secondaries, subopposite to alternate, diverging from midrib at angles of 40°, entirely straight or slightly convex in ascending course or convex near midrib, straight in lateral course terminating in strong marginal teeth; tertiaries trending at right angles to secondaries, forming with nervilles a reticulate background; margin simple-serrate to multiple-serrate; texture thick.

This species is named in honor of Dr. Raymond C. Moore, State Geologist of Kansas, with whose encouragement and assistance our study of the Tertiary floras of the High Plains has been made possible.

The material from the Middle Pliocene of California, referred by Dorf to *Ulmus brownellii*, is not distinguishable from our specimens. Like them, the California specimens are smaller, less slender, and less asymmetrical than *U. brownellii*. They resemble this Miocene species in having margins mostly simple-serrate, a character which was the principal basis for Dorf's reference of them to *U. brownellii*.

It seems possible that the specimens described by Lesquereux,⁴ and later noted by Knowlton,⁵ as *Alnus truncata* are not specifically distinct from our specimens of elm. None of the specimens of *U. moorei* have the base as truncate as Lesquereux's figure 8, but since we have not had an opportunity

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, 52, 1925.

² Rept. U. S. Geol. Surv. Terr., vol. 8, 169, pl. 33, figs. 5, 6, 1883.

³ Dept. U. S. Geol. Surv. Terr., vol. 8, 163, pl. 38, figs. 7, 8, 1883.

⁴ U. S. Geol. Surv. Terr., Rept., vol. 8, 150, pl. 28, figs. 7, 8, 1883.

⁵ U. S. Nat. Mus., Proc., vol. 51, 263, 1916.

to see this specimen, there is no certainty that it was correctly drawn. Many of the details, especially of drawings, in the earlier American reports, are subject to correction. In any event, the Lesquereux material seems referable to *Ulmus* rather than to *Alnus* on the basis of his description and figures; no living alders are known to have simple serrate margins. This marginal character related *Alnus truncata* to *Ulmus moorei*, but for the present they may be considered as distinct.

As above indicated, *Ulmus moorei* resembles *U. brownellii* from the Miocene at Florissant, Colorado, and the Crooked River of Oregon. The margins of both of these species tend to be simple-serrate, thus differing from those of any other fossil or living species of the genus in America. *U. parvifolia* Jacq. of northern China is the only living species which has a similar margin. Our specimens differ from *U. brownellii* in being smaller and less slender, and in having an essentially symmetrical base. A related fossil species, *U. shansiensis* from the Pliocene of Shansi Province, China,¹ resembles *U. moorei* more closely. In addition to having a generally simple-serrate margin, the leaves of this Chinese species are about the size and shape of *U. moorei* and have symmetrical bases. In view of the wide distance separating these fossil occurrences, there is no basis for referring them to the same species.

As stated above, none of the living American species of elm have leaves with conspicuously simple-serrate margins. It may be mentioned that certain small leaves of *U. crassifolia* resemble our fossil species both in shape and size, and that their margins may have some simple teeth. The leaves of this species average of larger size and are more asymmetrical than those of *U. moorei*. The habitat of *U. crassifolia*, on bottomlands and adjacent slopes through southern Arkansas and Texas, is suggestive of the assumed occurrence of our fossil species, on late Tertiary floodplains in regions of reduced rainfall.

Occurrence—Beaver County, Oklahoma, Loc. P-42; Logan County, Kansas, Loc. P-43.

Collection—U. S. Nat. Mus., Holotype, No. 39344; Paratypes, Nos. 39345-39348.

ORDER RANALES

Family CERCIDIPHYLLACEÆ

Genus CERCIDIPHYLLUM Sieb. & Zucc.

Cercidiphyllum crenatum (Heer) R. W. Brown

(Plate 7, figs. 4, 5)

Cercidiphyllum crenatum (Unger) R. W. Brown, Jour. Paleont., vol. 9, 575, pl. 68, figs. 1, 6, 8-10, 1935.

Grewia crenata (Unger) Heer, Fl. tert. Helv., vol. 3, 42, pl. 109, figs. 12-21, pl. 110, figs. 1-11, 1859.

This species represents the only genus in the Beaver County flora which does not occur in the High Plains at the present time. While it is abundant at many Miocene localities in the Great Basin, its absence from the intermediate situation at Florissant has suggested that its range during this epoch was limited at the east. The present record not only extends its known distribution, but adds to our knowledge of the fruits.

¹ Chaney, Bull. Geol. Soc. China, vol. 12, 131-132, pl. 1, figs. 4, 5, 1933.

Description—Fruits represented by two associated follicles, one complete; length 1.6 cm., width 0.5 cm.; a small portion of the stalk is preserved.

Cercidiphyllum may be considered to have been rare in Oklahoma during the Pliocene, since only two specimens have been collected. One of these is a leaf which shows typical nervation and margin; the other represents a pair of attached follicles. Since the former was found at Locality P-42 and the latter at Locality P-44, *C. crenatum* may be considered to have been generally distributed over the area, and its scarcity in the fossil record may be due not so much to rarity as to its occurrence on slopes removed from sites of deposition.

There is no previous record of this species or of other members of its family in North America after the Miocene.

Occurrence—Beaver County, Oklahoma, Locs. P-42, P-44.

Collection—U. S. Nat. Mus., Plesiotypes, Nos. 39349, 39350a, 39350b.

ORDER ROSALES

Family PLATANACEÆ

Genus PLATANUS (Tourn.) L.

Platanus aceroides Göppert

(Plate 7, fig. 12)

Platanus aceroides Göppert, Lesquereux, U. S. Geol. Surv. Terr. Rept., vol. 7, 184, pl. 25, fig. 4, 1878; Knowlton, U. S. Geol. Surv., Prof. Paper 101, 321, pl. 63, fig. 4, pl. 97, figs. 2, 3, 1917; Berry, U. S. Nat. Mus., Proc., 630, pl. 94, fig. 3, pl. 95, fig. 5.

Fossil leaves of sycamore, like those of living species, show such a wide range of variation in shape and margin as to suggest that there are fewer distinct species than have been recorded. In the case of the fossil species from western America, there may be noted a tendency toward reduction in size in later Tertiary time, when leaves with definitely cuneate bases are less conspicuous in the record than those with broadly cuneate to cordate bases. With these distinctions in mind, it has been the tendency of western palæobotanists in late years to refer the smaller, cordate-based leaves of the Miocene to *Platanus dissecta*. Larger, commonly cuneate-based leaves which characterize Eocene horizons have been referred to *Platanus aceroides*.

On this basis, the *Platanus* leaves from the High Plains are all referable to *Platanus dissecta*. But in the absence of any consistent procedure in separating these western species, the specific name applied by Berry to his Oklahoma specimens is here retained. These leaves are in no way distinct from those included under *Platanus dissecta* at numerous Miocene localities in the Great Basin.

The specimen figured on Plate 7 represents an immature leaf in which the normal lobation had not yet developed. The leaves at the Beaver Creek localities average much larger than those from Brown County, Nebraska, reflecting a more humid habitat. The comparative abundance of this species is indicated by the number of its leaves at the above localities and by the presence of wood associated with the leaf deposits in Brown County, and in beds of the same age in Cherry County, Nebraska.

Occurrence—Brown County, Nebraska, Loc. P-54; Beaver County, Oklahoma, Locs. P-42, P-44.

Collection—U. S. Nat. Mus. Plesiotype, No. 39351.

ORDER ROSALES

Family CÆSALPINIACEÆ

Genus GYMNOCLADUS Lamarck

Gymnocladus casei Berry

(Plate 6, fig. 7)

Gymnocladus casei Berry, U. S. Nat. Mus., Proc., vol. 54, 631, pl. 94, fig. 2, 1919.*Rhamnus lesquereuxi* Berry, U. S. Nat. Mus., Proc., vol. 54, 633, pl. 95, fig. 4, 1918.

Leaflets of this species are comparatively rare in our collections, as is the case with most of the thinner-leaved legumes in Tertiary and contemporary deposits. As pointed out by Berry, they average smaller than those of the living species, *G. dioica*, but are otherwise similar. However, the largest of our fossil specimens reaches a length of 5.5 centimeters, which is above average for the living leaflets examined by us. In view of the small number of specimens available for study, it seems desirable to make no generalizations based on the average small size of the leaflets of *G. casei*.

On the basis of our more complete material, several additions and corrections may be added to Berry's description. The leaflets range in length from 3.5 to 5.5 cm.; they are petiolate, with petiolules up to 4 mm. in length; most of them have long acuminate tips.

Of the two living species of *Gymnocladus*, the North American *G. dioica* ranges into western Oklahoma, though not as far west as Beaver County. The Chinese species, *G. chinensis*, has smaller and thicker leaflets and lives under somewhat warmer climatic conditions than the American species. Both on the basis of its leaflets and geographic occurrence, the fossil species shows a close relationship to *G. dioica*.

The leaves described as *Rhamnus lesquereuxi* from the Beaver County flora do not appear, upon examination of two of Berry's specimens, to be distinguishable from *Gymnocladus casei*. No opportunity has yet been had to examine the Lesquereux specimens of *Rhamnus notatus* (?) from the Florissant, which as illustrated appear also to be identical. So for the present only the Beaver County *Rhamnus* is placed in synonymy with *Gymnocladus casei*.

Occurrence—Beaver County, Oklahoma, Locs. P-42, P-44.

Collection—U. S. Nat. Mus., Plesiotype, No. 39352.

ORDER SAPINDALES

Family ACERACEÆ

Genus ACER L.

Acer negundoides MacGinitie

(Plate 7, figs. 10, 11)

Acer negundoides MacGinitie, Carnegie Inst. Wash. Pub. No. 416, pl. 11, figs. 2, 3, 1933; LaMotte, Carnegie Inst. Wash. Pub. No. 455, V, 1935.

This species, based on seeds, has been recorded and figured by MacGinitie from the Upper Miocene of southwestern Oregon. Similar seeds and abundant, though fragmentary, leaflets were collected by Chaney 15 years ago from late Tertiary deposits in northern Oregon, near The Dalles. More recently LaMotte has described fruit and a leaflet from the Upper Miocene of Nevada. All of this material appears to be specifically identical with

the specimens from Beaver Creek, which comprises a single seed and an incomplete leaflet.

Several varieties of the living *Acer negundo* have been recorded, but the differentiating characters are not sufficiently marked to make possible their recognition in the fossil material at hand. It seems desirable therefore to refer all of the western specimens to a single species, although varietal differences similar to those of the living box-elders may ultimately be recognized.

As in the case of the living species, *A. negundoides* was widely distributed in western America; but except at the northern Oregon locality it is nowhere abundant in the late Tertiary record.

Occurrence—Beaver County, Oklahoma, Loc. P-44.

Collection—U. S. Nat. Mus., Plesiotypes, Nos. 39353, 39354.

ORDER SAPINDALES

Family SAPINDACEÆ

Genus SAPINDUS L.

Sapindus oklahomensis Berry

(Plate 7, figs. 1-3)

Sapindus oklahomensis Berry, U. S. Nat. Mus., Proc., vol. 54, 632-633, pl. 95, figs. 1, 2, 1918.

On the basis of material which was less complete, judging from the specimens figured, than that in our collections, Berry referred leaflets of *Sapindus* to this species, as distinguished from several others recorded from the Tertiary of western America. Since then several additional species have been described. Recently LaMotte has studied *Sapindus oregonianus* Knowlton as represented in the Mascall formation of Nevada, Idaho and Oregon.¹

These later studies suggest that the Miocene species of *Sapindus* have been unduly multiplied. The species described by Knowlton as *Sapindus oregonianus* may ultimately be considered to include most or all of the Miocene forms from western America, since it shows a range in size and shape which appears to include many specimens otherwise named. The available material of *S. oklahomensis* falls within the range of its leaflets. However, it seems desirable, in view of the considerable geographic gap in range between these species, to retain our material under the name *S. oklahomensis*.

Occurrence—Beaver County, Oklahoma, Locs. P-42, P-44.

Collection—U. S. Nat. Mus., Plesiotypes, Nos. 39355-39357.

ORDER EBENALES

Family SAPOTACEÆ

Genus BUMELIA Sw.

Bumelia florissanti Lesq.

(Plate 6, fig. 6)

Bumelia florissanti Lesquereux, Rept. U. S. Geol. Surv. Terr., vol. 8, 174, pl. 34, fig. 4, 1883.

A single specimen from Beaver Creek differs from the Florissant specimens only in having a more slender base, to which a long petiole is attached. The leaves from both localities are well within the range of variation of the

¹ Carnegie Inst. Wash. Pub. No. 455, 37-38, pl. 1, figs. 2, 3, 5, pl. 2, figs. 1-4, pl. 3, figs. 1, 2, 4, 5, 1935.

modern related species, *B. lanuginosa* Pers. This species ranges into western Oklahoma at the present time, where it is a border member of the valley forest.

Berry has described as *B. oklahomensis* an incomplete leaf from the Beaver County deposits. Examination of the type gives us no basis either for placing it in synonymy above or for including it in the present list of species. It is too poorly preserved to show any significant characters, and as figured is unlike the leaves of *B. florissanti* or of any of the living American species.

Occurrence—Beaver County, Oklahoma, Loc. P-44.

Collection—U. S. Nat. Mus., Plesiotype, No. 39358.

ORDER EBENALES

Family EBENACEÆ

Genus DIOSPYROS L.

Diospyros pretexana n. sp.

(Plate 7, figs. 6-8)

Diospyros brachysepala Al. Braun., Knowlton, U. S. Nat. Mus., Proc., vol. 51, 285, 1916; Berry, U. S. Nat. Mus., Proc., vol. 54, 635, pl. 95, fig. 3, 1918.

The presence of *Diospyros* in the Beaver Creek flora was recognized by Berry, who referred his material to the widely distributed species *brachysepala* on the basis of its resemblance to material from Florissant which had been so identified. While the Beaver County specimen figured by Berry shows a general resemblance to the Florissant specimens, it differs from them in the significant character of being much smaller. The specimens of *Diospyros* in our collections are likewise small, and although they are somewhat more bluntly tipped than Berry's specimen, they are all clearly referable to the same species.

A survey of the Tertiary species of *Diospyros* described from North America indicates a trend toward reduced size from the Eocene to the Miocene. Several early Tertiary species are known, of which *D. oregona* of the Goshen flora is the largest.¹ *D. brachysepala*, while recorded from older Tertiary horizons, seems most characteristic of the Miocene on this continent. It is of medium size, the figured specimens from Florissant averaging 6.5 centimeters in length. Another Miocene species, *D. elliptica*, is fairly common in the Mascall and other late Miocene deposits of the Great Basin; its leaves average the same size as the Florissant specimens of *D. brachysepala*, although certain smaller specimens range down in size to less than 4 cm. It seems probable that the Miocene leaves from the Great Basin and Florissant represent the same species and, as Berry has suggested, the specific name *brachysepala* is not appropriate.

Our Oklahoma specimens average 3.5 cm. in length, and none of them is as large as the average of the Miocene species to the north. They correspond in size with the leaves of *D. texana* of southwestern Texas and adjacent Mexico, a species which is distinguished from the more widely ranging *D. virginiana* on the basis of the small size of its leaves. Like the leaves of *D. texana*, our fossil specimens have bluntly obovate tips and relatively thick texture, and their relationship to this living species is apparent. This relationship is considered an adequate basis for referring the Beaver County leaves to a distinct species *pretexana*. The climatic requirements of *D. texana* are so distinctive as to throw much light on the type of environment occupied by its Pliocene equivalent in the Beaver Creek flora.

¹ Chaney and Sanborn, Carnegie Inst. Wash. Pub. No. 439, 92-93, pl. 36, figs. 2-4, 1933.

Description—Leaves varying from elliptical to obovate, with the apex tapering to a blunt tip, commonly emarginate; base varying from sharply cuneate and slightly inequilateral to bluntly rounded and equal; length from 2.6 to 4.3 cm., averaging 3.5 cm., width from 0.8 to 2.0 cm., averaging 1.4 cm.; petiole, when preserved, short (5 mm.) and stout, somewhat swollen proximad; midrib firm, slightly curving; secondaries opposite in the basal, alternate in distal half of leaf, diverging from midrib at angles of 45° and curving toward the apex abruptly near the margin to meet the secondary above, forming loops; tertiary veins where preserved conspicuously reticulate, entering into the marginal loops; margin entire; texture firm.

The genus *Diospyros* is at present largely distributed in the tropics. *D. virginiana*, the Miocene equivalents of which, *D. elliptica* and *D. brachysepala*, were wide-ranging in western America, is now found as far north as Connecticut, but it is more characteristic of the southern United States. The genus is no longer living in the western United States, where it appears to have become extinct at the end of the Miocene along with a large group of broad-leaved, deciduous genera which have survived in eastern North America and eastern Asia, in regions of summer rainfall.¹ In the Pliocene occurrence of *D. pretexana* in Oklahoma, there is evidence of the differentiation by late Tertiary time of the smaller-leaved type of persimmon which has survived in regions of reduced rainfall.

Occurrence—Beaver County, Oklahoma, Locs. P-42, P-44.

Collection—U. S. Nat. Mus., Cotypes, Nos. 39359-39361.

ORDER GENTIANALES

Family OLEACEÆ

Genus FRAXINUS L.

Fraxinus ungeri Lesquereux

(Plate 6, figs. 8-10)

Fraxinus ungeri Lesquereux, Rept. U. S. Geol. Surv. Terr., vol. 8, 171, 1883; Knowlton, U. S. Nat. Mus., Proc., vol. 51, 286, pl. 22, fig. 3, pl. 23, figs. 1, 2, 1916.

The material originally described as this species from Florrissant by Lesquereux comprises three specimens, one of which, as Knowlton has properly indicated, does not appear to be conspecific with the others. Without seeing this specimen, no final opinion can be expressed, but as figured it closely resembles *Umbellularia* in shape and nervation. The other two specimens are correctly referred to *Fraxinus*; they represent somewhat smaller leaflets than the average size of the Beaver Creek specimens, with which they seem specifically identical. It should be noted that Lesquereux's description states that the margin of this species is "very entire"; the margins of our specimens show occasional small but unmistakable dentations along the distal portions. In view of the more adequate material now available, the species will be re-described.

Description—*Terminal leaflets* ovate, apex acuminate, base sharply cuneate and slightly asymmetrical; length 7 to 8 cm., width 3.5 to 4 cm., maximum width proximad to middle of leaf; petiolule, where preserved, short, stout; midrib ridged, strong, tapering sinuous; secondaries in basal portion of blade opposite, but alternate distally, diverging from midrib at angle of 50° to 60°, curving gently in their ascending course where at the margin they turn up abruptly or bifurcate into apical and basal branches which run into the margin or join similar veins from adjacent secondaries to form

¹ LaMotte, Carnegie Inst. Wash. Pub. No. 455, V, 1936.

irregular loops; a small pair of basal secondaries extends apically for a distance of 1 to 2 cm. to form a fine but distinct marginal vein; tertiaries irregularly trending at angles of 60° to 90°, commonly obscured in the reticulate background; occasional small intersecondaries arise from midrib and anastomose with tertiaries; margin entire in the basal half, with a few fine dentations toward the apex; texture firm.

Lateral leaflets ovate to lanceolate, apex acuminate, base bluntly cuneate, nearly symmetrical to asymmetrical; length 4.5 to 6.0 cm., width 2.2 to 3.0 cm.; petiolule, where preserved short, stout, swollen proximad; midrib firm, tapering, slightly falcate; secondaries subopposite in basal portion to alternate in distal half of blade, diverging from midrib at angles of 40° to 60°, otherwise similar to those of terminal leaflets; tertiary venation where preserved similar to that of terminal leaflets; margin entire in basal half, slightly dentate in distal part of some specimens; texture firm.

A close similarity is apparent between *Fraxinus ungeri* and the living *F. americana*. This species is widely distributed in the eastern United States, extending westward into northwestern Oklahoma and eastern Texas, where it occupies river valleys. Certain of our specimens also show a resemblance to *F. oregona*, now living in the western United States. Since the range of variation in the leaves of *F. americana* is sufficient to include all of the leaflets in the Beaver County collections, there is no occasion to distinguish two fossil species. The resemblance to *F. oregona* is mentioned here only to suggest the possibility that the latter may represent a regional segregate of *F. americana*.

Among other fossil species, *F. ungeri* closely resembles *F. denticulata* Heer from the Miocene of the John Day Basin and Yellowstone Park, as well as from older horizons in Montana and Greenland. It is probable that the Miocene specimens referred to *F. denticulata* may be more properly considered as identical with *F. ungeri*.

No less than eight species of *Fraxinus* have been described from the Florissant flora, a number equaling that known from the whole of the United States east of the Mississippi at the present time. Beyond mentioning at this point that these species seem to be unjustifiably multiplied, and that one of them appears to be properly referable to the genus *Celtis*, no comment need now be made on the need for revising this and other genera of the Florissant flora.

Occurrence—Brown County, Nebraska, Loc. P-54; Beaver County, Oklahoma, Loc. P-42.

Collection—U. S. Nat. Mus., Plesiotypes, Nos. 39362-39364.

INCERTÆ SEDIS

Genus PHYLLITES Brong.

Phyllites sp.

(Plate 7, fig. 9)

Description—Leaf lanceolate, tapering to a rounded tip, base cuneate, nearly symmetrical; length 2.6 cm., width 0.6 cm., greatest in basal third of blade; petiole firm, incomplete; midrib firm, tapering, slightly sinuous; secondaries alternate, diverging from midrib at angles of 60°, curving abruptly apically to run nearly parallel to margin, a basal pair emerge close to point of petiole attachment and course parallel to margin in basal quarter of blade, all looping broadly into adjacent secondaries; tertiary venation where preserved, reticulate; margin serrulate; texture firm.

Occurrence—Beaver County, Oklahoma, Loc. P-44.

Collection—U. S. Nat. Mus., Holotype, No. 39365.

LOWER PLIOCENE VERTEBRATE FOSSILS FROM THE OGALLALA FORMATION (LAVERN ZONE) OF BEAVER COUNTY, OKLAHOMA

BY CURTIS J. HESSE

(With ten text-figures)

In recent years, many vertebrate palaeontologists of this country have concentrated their efforts on a study of the Pliocene. The increment of knowledge of this phase of past life has increased at a rapid rate, with the result that certain perplexing problems of an earlier day now appear to be solved.

Prior to the discovery of the Snake Creek Quarries in 1909, by Matthew and Cook, the Pliocene was the least known of the North American Tertiary vertebrate faunas. The Snake Creek collections were first thought to contain only Lower Pliocene fossils and were described as such by the discoverers (Matthew and Cook, 1909). For some years before this discovery, Dr. John C. Merriam had been investigating the Tertiary sequence of the Pacific Coast, where small, fragmentary vertebrate faunas had been found, often intercalated with the marine beds. Merriam's material was, in most cases, unmixed, and basing his conclusions on this West Coast sequence, he suggested (1917, 437) that the Snake Creek collections contained elements of both Miocene and Pliocene age (See Matthew, 1918, foot-note 2). It has since been shown that this was the correct interpretation (Matthew, 1918, 1924), and that the fauna of these famous quarries is both Miocene and Pliocene in age. Future work may show even greater complication than this, for certain localities at Snake Creek seem to contain faunas representing different stages of the Pliocene (Matthew, 1924, 72).

The description of this mixed material as Lower Pliocene has resulted in confusion and misunderstanding in later finds of similar age. It has been the source of some difference of opinion as to the age of other faunas and has also shown that some other faunas were, like the Snake Creek, mixtures of different ages (Stirton and McGrew, 1935, 128).

It is, accordingly, desirable to record such faunas as the one described in this report, incomplete though it be, since there is no indication of mixture with forms of a different age. Then, too, the Beaver County fossil localities are exceptional in that vertebrates, land plants and diatoms all occur within a small area which allows a summation of these various lines of evidence as to age and general ecology of these deposits.

The vertebrate fossils described in the following pages were collected at two different times. The University of Kansas collection was made in

August 1931, by a field party from the Museum of Palæontology of that Institution. This locality was visited at the suggestion of M. K. Elias of the Kansas State Geological Survey, who wished to obtain an additional collection of the flora of this area. The fossil vertebrates were discovered at a nearby outcrop (Beaver Quarry), but lack of time prevented this party making an extensive collection of them. Through the courtesy of M. K. Elias, and of H. H. Lane of the Department of Zoology at the above institution, the vertebrate material was sent to the writer for description. As the study of this small fauna progressed, it became more evident that the locality is an important one because of its association with the plant material. For this reason, it was again visited (at the suggestion of the writer) in the summer of 1935 by a field party of the Museum of Paleontology of the University of California. The collection made by this second party contains most of the better specimens and was collected at two localities. It is important since it was secured both below and above the plant-bearing beds.

SUMMARY OF INVESTIGATIONS IN BEAVER COUNTY PRIOR TO 1930

Fossil leaves from this locality were noted as early as 1889 by F. W. Cragin (1889, 67); but it was not until 1891 that the locality was visited and collections made. Cragin, in his report on this area (1891, 29), gave an excellent summary of the local geology, listed seven species of leaves and six species of diatoms which had been determined for him by F. Walls. With reference to the age of these beds, Cragin found the distal end of a camelid radio-ulna in the leaf-bearing strata and a tooth of *Hippotherium speciosum* (*Hippotherium speciosus* now considered *nomen nudum* Osborn, 1918, 129). Cragin's specimen is probably the small species of *Nannippus* referred to below) in the stream immediately below. In discussing these finds, he stated:

"The ulno-radius itself, however, settles the age of the leaf-bearing marl. Whatever be the genus or species, it indicates an ungulate limb of such a kind and degree of specialization as, taken in connection with the size, would be inconsistent with its reference to any epoch earlier than the Loup Fork, its stratigraphic relation to the associated Loup Fork *Hippotherium*-bearing mortar clearly shows."

The above statements are quite correct and additional investigations in this area have supplied only greater detail. Two years after Cragin's paper appeared, the Beaver area was visited by E. C. Case, who made a collection of the flora and the following year published a brief account of the general geology with special reference to the "Chalk outcrops" (Case, 1894, 143-147). The specific locality was not again noted until E. W. Berry (1918, 629) described a small flora collected there (again by Case) and concluded that it was of Upper Miocene age.

The Tertiary deposits of the general region of Beaver County, Oklahoma, consist of a blanket of calcareous sands, clays and gravels of a varying degree of induration and thickness. In their general character and relations, they are the same as beds in the Ogallala formation (Darton, 1899, 178-179), which have been mapped to the northern border of Beaver County (Darton, 1905). In discussing the geology of Oklahoma (1905, 79) and the Panhandle of Texas (1906, 24-30), C. N. Gould suggests that the Tertiary of these areas is the same as that extending northward into Kansas and Nebraska (*i.e.* Ogallala). Later, Rothrock (1925, 68) referred to the Tertiary rocks of Cimarron County, Oklahoma, under the name Nussbaum¹ Ogallala. Gould and Lonsdale (1926, 68) state that the Tertiary of Texas County, adjacent to Beaver on the west, is the same as the general Tertiary of Kansas, Colorado and Nebraska. In the light of these opinions, it seems beyond doubt that the Tertiary of Beaver County may be referred to the Ogallala formation of Darton.

Unfortunately, the term "Panhandle formation" was introduced by J. W. Gidley (1903, 634) for the Tertiary grits of the Llano Estacado, the entire area bordering Beaver County on the south. This usage was followed by Matthew (1925, 221), Sellards *et al.* (1933, 767), and is today recognized by most of the geologists working in this area (letter from F. B. Plummer to the writer, May 28, 1935).

There is no reason to believe that the above names are applied to separate stratigraphic units, and it seems fairly certain that both refer to the same formation. Therefore, the academic question of which name to apply must be settled by priority, usage and definition. The writer, in this and other reports, follows the usage of the U. S. Geological Survey in recognizing the name Ogallala in place of Panhandle (See Darton, 1928, 58; Wilmarth, 1930, Chart I; 1931, Chart I; Hesse, 1935b, 82.)

ORIGIN AND GENERAL ECOLOGY OF THE OGALLALA FORMATION (LAVERN ZONE) IN BEAVER COUNTY, OKLAHOMA

Baker (1915), Sellards, *et al.*, (1932, 769) and others have set forth the general conditions under which the Later Tertiary terrestrial deposits of the high plains of Texas were laid down. Since this area is immediately adjacent to Beaver County, Oklahoma, on the south, essentially the same conditions probably apply to the latter. For a detailed, critical discussion of the environment the reader is referred to the first part of this paper in which the climatic, ecologic and distributional evidence of this and allied floras are set forth.

Their conclusions are quite in keeping with the general conditions suggested by Sellards (1932, 769), but the Texas region has but scanty evidence of trees. Along with these two accounts is the opinion of Waite

¹ U.S.G.S. Committee on geologic names has restricted Gilbert's "Nussbaum formation" (1897, 3) to its type locality and adjacent areas—Letter from G. M. Wilmarth, April 15, 1935.

(MSS. in Gould and Lonsdale, 1926, 33) as to the conditions under which the "soft white limestone" of Beaver County was deposited:

"It is the opinion of the writer that the formation represents a series of small lakes, perhaps similar to the present lakes in Northern Indiana. This suggestion is tentatively made for the reason that the formation is scattered and has a variation in lithologic character even though the outcrops are only a short distance apart. The fauna, too, indicates small separate bodies of water. For instance, at one locality, clam shells are found in abundance and not in others. In one locality, fossils were much larger than in others. At another place, a great number of leaves were found. A two-inch seam of peat was found at still another. These facts would indicate small bodies of water either isolated or connected in which the conditions in one place were different in another and thus the cause for variety of fossils both in size and species."

While I am not fully in accord with all of the above statement, I do believe that the suggested conditions of deposition are, in the main, correct. They are not contrary to the ideas set forth by Sellards and are further born out by the high diatomite content of part of the beds. In their essentials, the conclusions cited above are much the same as those reached by M. K. Elias (1931, 141) after a detailed study of the Ogallala formation as exposed in Wallace County, Kansas, some two hundred miles northwest of the area covered above.

Unfortunately, the seeds of fossil grasses, with which Elias (1935, 29) has been able to zone the later Tertiary beds of the high plains, were not found in the marls at this locality. He informs me¹ that the "Mortar Beds" (i.e. Ogallala) which cover the highest hills in Beaver County contain typical seeds which place them in his "Biorbia Zone" (See also Elias, 1935, 32) and are capped with the Algal limestone noted (1931, 136) by him in Wallace County, Kansas. This zone is characterized, in other areas, by a Middle Pliocene vertebrate fauna (Feldt Ranch, Beecher Island, Edson, Rhinoceros Hill); but so far in Beaver County itself none of this more advanced fauna has been collected. Elias further states that some of the fossil vertebrates described here, as well as the plant remains referred to above, were collected in a bed of diatomaceous marl, which outcrops low in the valleys. These diatomite beds are, furthermore, strongly folded, while those of the "Biorbia Zone" overlying them are horizontal.

DISCUSSION OF LOCALITIES AND DESCRIPTION OF MATERIAL

The vertebrate fossils forming the basis of this report were collected at two main localities and several scattered individual finds. Since some significance is attached to each of the two main localities, it seems wise to discuss the collection made at each under separate headings.

Camp Creek Locality—N.W. $\frac{1}{4}$ of S.E. $\frac{1}{4}$ of Sec. 28, T. 4 N., R.25 E., E.C.M.; U.C. loc. No. V3517. On the right (west) bank of Camp Creek,

¹ In a letter, January 1, 1934.

two incomplete upper horse teeth were collected. They were taken from a red sandstone which contains many small lime nodules. This sandstone is underlain by a well-indurated grayish sandstone, three to four feet thick, resting directly on the Cloud Chief formation (Permian).

Fauna—Unfortunately, the two equid teeth collected here (U.C. Mus. Pal. No. 32804) are shattered and incomplete in many details. Nevertheless, certain points regarding their structure may be made out. The teeth are high-crowned (36.2 and 32.3 mm.) in proportion to their size and, in general, have a well-advanced appearance. The protocones of both seem to be isolated; but it is difficult to see this character. The styles on the outer side are light, and the mesostyle does not "pinch in" above its base as one would expect in *Merychippus*. Only the major features of the crown pattern may be made out, and these are insufficient to determine the genus. The height of crown, lightness of the mesostyle and probable isolation of the protocone are points which, in my opinion, place these teeth in the genus *Nannippus*. They are similar, in all probability, to the teeth collected in the other two localities. On this evidence, then, we may questionably assign the beds at this locality to the Lower Pliocene.

Cragin locality—Near center of Sec. 3, T.3 N., R.25 E., E.C.M.; U.C. loc. V3516. An exposure of diatomaceous marl on the east side of Gyp Creek, slightly northwest of the center of Section 3. It is very probable that this is the "Alpine locality" from which Cragin collected his flora and fauna in 1891. It is a prominent exposure (See Gould and Lonsdale, 32, pl. VII), and the only one in the vicinity from which leaves may be collected in anything like abundance. This is most certainly the locality mentioned by Case, from which he made his collection in 1894 and later, the one described by Berry. Gould and Lonsdale quote at length (1926, 33) from a manuscript by V. V. Waite regarding the ledge of "soft white limestone" outcropping at various points in Beaver County. Mr. Waite proposed the name "Lavern formation" for this bed; but while it does not seem to be of sufficient importance to warrant a formational name, it could be accurately designated as Ogallala formation (Lavern Zone).

The diatomites at this locality are of an unknown thickness since the top of the bed has been eroded away. The beds dip at a low angle to the north and west, thus passing under the Beaver Quarry from which the larger collection of vertebrates came. Beneath the diatomites, about 7 or 8 feet, is a layer of greenish, sandy clay from which the vertebrates described below were collected.

DESCRIPTION OF THE FOSSIL VERTEBRATES COLLECTED AT THE CRAGIN LOCALITY

PISCES

In the diatomite marl directly associated with the leaves, there are many spines, vertebræ and scales of fish. These all seem to represent one type; but unfortunately most of the material is indeterminate. One specimen

(U.C. Mus. Pal. No. 32811) is that of a badly distorted and incomplete skull of one of these fishes. In general, the size and the ctenoid scales of this specimen suggest some member of the Percidæ (Cragin, 1891, 29), a form much in keeping with the ecological background already set forth. These fishes were evidently common at the time of deposition of the diatomite.

PERISSODACTYLA

EQUIDÆ

It has frequently been noted that fossil equids are by far the most common mammalian fossils in the later Tertiary of the high plains. The wealth of material representing this group probably explains the great detail with which it has been studied. In general, the evolutionary trends within the group have been known for over fifty years; but many of the complex interrelationships of certain genera and species remain to be worked out. Unfortunately, most of the genotypes were selected over fifty years ago when both the geographic and stratigraphic positions of these finds were uncertain. Today the exact stratigraphic and geographic position of these early types can be determined only by placing them in faunas where similar material is now known to occur. Then, too, most of the old specimens are very fragmentary, at best a few teeth, and those often deciduous, making it difficult to refer much of the material found today (whose individual variation is considerable) to the first described forms.

It is evident from the above that in studying the fossil equids of the later Tertiary, many errors are likely to be made. Incorrect stratigraphic reference of types, and most of all incorrect reference of new, more complete material to old well-established names are possible sources of error. One must pass judgment upon the work done by the others in recent years and therefore conclusions reached often become a matter of individual opinion. At any given time, it is not possible to do more than discuss these forms as one understands them, pointing out their apparent relationships and systematic position; the results of such studies must be left to stand the test of time.

The following paragraphs, as well as those in other parts of this report, dealing with the horses, are the results of a special investigation of this group that has been carried on at the University of California for the past few years. Most of the observations and suggestions on the phylogeny of the equids, set forth here, are conclusions reached by R. A. Stirton after a detailed study of this interesting and important group of genera.

Calippus martini n. sp.

Type—Upper left dentition P2 M3, U.C. Mus. Pal. No. 32814.

Type locality—Cragin Quarry, Sec. 3, T.3 N., R.25 E., E.C.M. Ogallala Pliocene of Beaver County, Oklahoma. (See fig. 1.)

Referred material—The type; No. 32814; a right lower jaw, dpI-4, MI; No. 32815, a right lower jaw and probably a few skeletal elements, all in the University of California Museum of Paleontology.

Systematic note—The genus *Calippus* was first defined as a subgenus of *Protohippus* by Matthew and Stirton (1930, 354), to include certain species referred to *Protohippus*, but which were not believed to be typical of that genus. This subgenus covered, in a sense, the group II of this genus noted many years ago by Osborn (1918, 127).

In working over the *Protohippus ansæ* material from Texas, as well as that from other Pliocene localities representing other species, it seemed a more logical arrangement to refer these younger forms to a separate genus. This was necessary since the genotype of *Protohippus*, *P. perditus*, is probably Upper Miocene in age and is much more closely related to the advanced merychippine forms and to *Pliohippus* than it is to the Pliocene forms referred to *Calippus*. *Calippus* was then proposed as a genus (Stirton, 1935 b, 382), with *C. placidus*, the genotype.

Description—*Upper dentition* (fig. 1). In contrast to *Calippus ansæ*, its nearest relative, the upper cheek teeth of *C. martini* exhibit the following

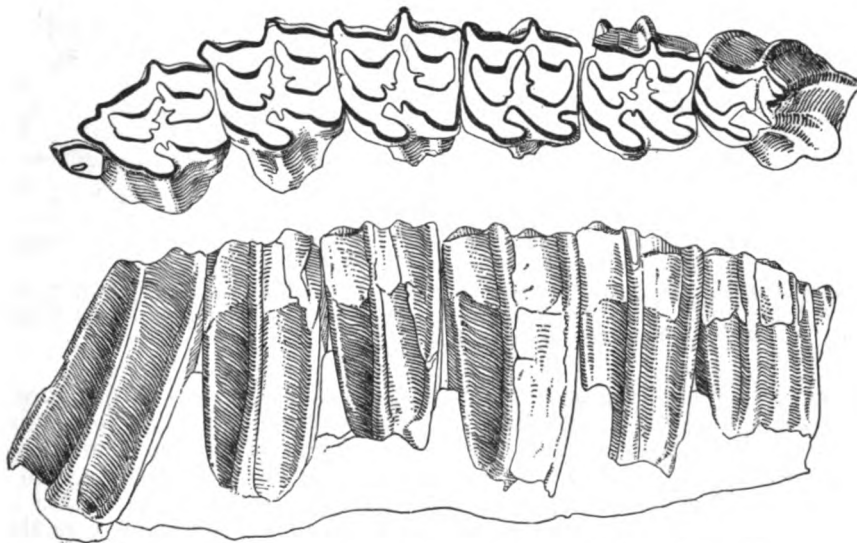


FIG. 1.—*Calippus martini*. Type specimen, upper left dentition P4 to M3, U.C. Mus. Pal. No. 32814. From the Cragin Quarry, Ogallala Lower Pliocene, Beaver County, Oklahoma. Drawn natural size by Owen J. Poe.

characters: The two forms are approximately the same size, the crowns of the teeth of *C. martini* being slightly larger. *C. ansæ* is more hypsodont and the teeth are less curved, while those of the Oklahoma form are more *Pliohippus*-like in curvature. The outer styles are much lighter in *C. martini*, especially the metastyle. In crown pattern, the premolars of *C. martini* have a definite plicabillin fold, the enamel lake borders are more complicated, the protocone more broadly joined to the protoloph, and the post protoconal valley tends to be more widely open. The protocone on *C. martini* is more rounded on its buccal side and shows no flattening as

in *C. ansæ*. The Oklahoma species may be readily distinguished from *C. placidus* on its greater size and in the curvature of the teeth.

Lower dentition.—Unfortunately, the lower dentition of *C. martini* is represented by two lower jaws with deciduous teeth (fig. 2). The first two

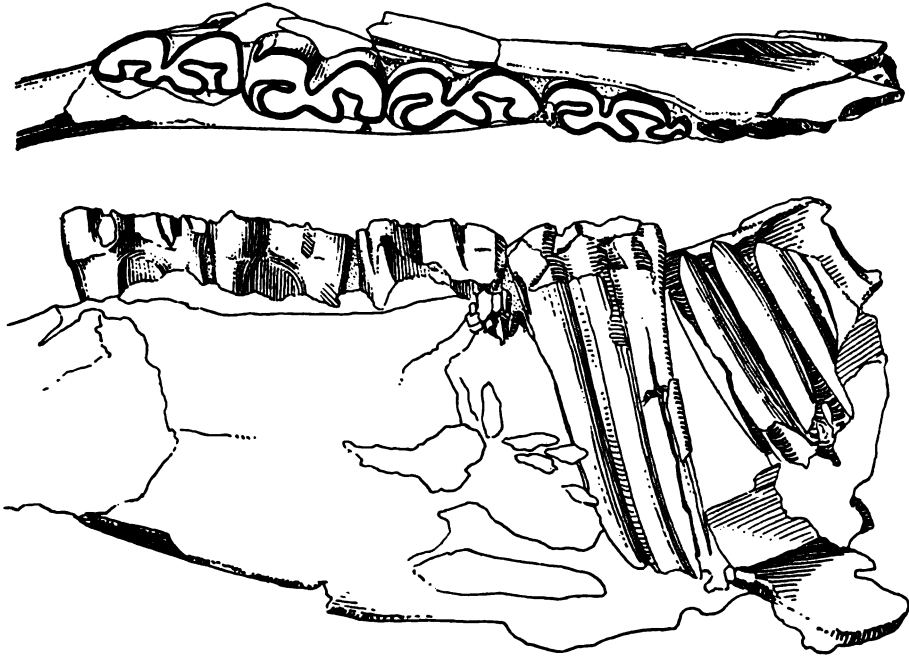


FIG. 2.—*Calippus martini*. Topotype specimen. Right lower jaw, dp 2-4, MI-2, U.C Mus. Pal. No. 32818. From the Cragin Quarry, Ogallala Lower Pliocene, Beaver County, Oklahoma. Drawn natural size by Owen J. Poe.

molars are just erupting, and upon them the following points may be based: they are hypsodont, less so than *C. ansæ*, but more than in any known species of *Merychippus*. The metaconid and metastylid are rounded and widely separated by a shallow valley that fades away toward the base of the crown. The protoconid and hypoconid are rounded. These teeth are remarkably high-crowned in proportion to those of *C. ansæ*, more so than one would expect, since the two faunas are probably separated by considerable time.

Discussion.—*Calippus martini* is most closely related to *C. ansæ*, of the Hemphill fauna. In the characters which separate the two, height of crown of upper molars, pattern, etc., *C. martini* is distinctly more primitive. *Calippus placidus* is a much smaller, more primitive form, foreshadowing in some measure the characters of *C. martini*. There can be no question that the upper teeth of the Oklahoma species and *P. perditus* are very close, so close that if the lower teeth were unknown, the two would be considered the same.

? *Nannippus* sp. ?

Referred material.—A left lower jaw dp 2-4, MI, No. 32818; several worn lower teeth, the symphysis of a lower jaw and a few skeletal elements.

The above material is incomplete and the larger part of it not diagnostic of the genus. The lower jaw is that of a young animal, and has so suffered from the vicissitudes of time that few of the characters may be determined. It is slightly smaller than the lower jaw of *C. martini* from the same quarry and, in proportion, its teeth are less high-crowned. The metaconid and metastylid are somewhat elongate and separated by a wide but shallow valley. So far as may be determined, this valley carried to the base of the teeth. The remainder of the specimens may readily be duplicated in the *Nannippus* material of the Clarendon fauna.

? *Neohipparion*

Referred material—Two lower teeth and a proximal and median phalanx, No. 32821.

These specimens seem a little too large to be placed in either of the above genera. The lower teeth are definitely of the *Hipparion* group on the separation of the metaconid and metastylid. The two phalanges are slender, more so than any of those of pliohippids in allied faunas. It would seem probable that these fragments represent the same *Neohipparion* as that collected in the Beaver Quarry.

Teleoceras sp.

Referred material—An astragalus, No. 32819.

A rather small, left astragalus of a rhinoceros is readily referable to the above genus. Matthew (1932, 429) has listed the characters which may be used to separate the astragali of *Aphelops* from *Teleoceras*, the two most common Pliocene genera. The astragalus described here is definitely teleocerine on the basis of the shortness of its trochlear surface (antero-posteriorly), fibular facet less marked, astragalo-calcaneal facet flattened and less elongate, and the inner edge of the trochlae rounded. It is so much smaller than any of the *Teleoceras fossiger* astragali in our collections that it seems almost certain that it does not represent that species. The Pliocene species of the genus *Teleoceras* are all large animals about the size of the common *T. fossiger*. The Miocene forms *T. mendicorutus* and *T. minor* are distinctly smaller in size, suggesting the possibility that an unrecognized species of *Teleoceras* may exist in the Lower Pliocene of the High Plains.

? *Blastomeryx*

Referred material—A proximal phalanx and a fragment of the shaft of a metatarsal.

Although the above material is insufficient for an accurate generic diagnosis, it is certain that it belongs to a small artiodactyl. It is smaller than similar elements described by the writer (Hesse, 1935, 308) under the name *Capromeryx altidens*, and seems more in keeping with some species of the *Blastomeryx-Merycodus* group.

Beaver Locality—This locality is on the Bennett Ranch, 9½ miles east and 3 miles south of Beaver City, Beaver County, Oklahoma. It is on the right (east) bank of Gyp Creek, which flows northward into the main stream called Beaver River or the North Fork of the Canadian. The small quarry (U.C. loc. No. V 3515) from which the specimens were taken lies near the section line between Sec. 3, T.3 N., R.25 E., and Sec. 34, T.4 N., R.25 E., E.C.M. The majority of the material forming the basis of this report was collected here. It was first opened in 1931 by the University

of Kansas party under the direction of Mr. C. W. Hibbard, and the material listed in the following pages obtained for that institution. After a study of this material, the area seemed to warrant further investigation and the University of California party obtained considerable additional information.

The quarry itself is in the low bank of Gyp Creek, its area not large, and worthwhile specimens are few and far between. The majority of the specimens came from an excavation about 15 feet long and were confined to a zone about 2 feet thick. There were random finds outside this layer; but they were not common. A blue-gray clay and a grayish sand make up most of the bank, but even this varies considerably within the small area. The entire bed dips, at a low angle, to the northwest, thus overlying the diatomites of the Cragin locality already described.

Beside the above, there were certain other specimens found which were not from the Beaver quarry, but which were within that area. These have been termed sites and are represented in the collection by only one or two specimens. The following sites are recognized:

- SITE 1. Sec. 34, opposite camp, below (downstream) the Beaver Quarry. An M3 of *Nannippus* and the distal phalanx of a rhinoceros were picked up in the stream bed. These specimens were not in place, but had washed out of some of the fossiliferous beds upstream.
- SITE 2. Sec. 34, on the right bank of Gyp Creek, about 50 yards below the Beaver Quarry. Three lower teeth of *Nannippus*. This is a possible source of the material picked up at Site 1.
- SITE 3. Sec. 3, 100 yards upstream (south) of the Beaver Quarry, on the right bank, about 6 feet stratigraphically below the level of the Quarry. A lower jaw, a maxillary and some teeth of *Neohipparion*, collected, in place, from a reddish sand.
- SITE 4. Sec. 3, on the right bank of Gyp Creek, farther upstream from Site 3, approximately 15 feet below the level of the Beaver Quarry. A lower jaw of *Alticamelus*, and the incomplete carapace and plastron of a tortoise were collected here from the reddish sands.

The material collected at these sites is regarded in this report as a part of the fauna of the Beaver Quarry and is described, in its proper place, as such. In general, the beds upstream from the main Quarry are stratigraphically below the main fauna, and those downstream are above. However, the dip of the beds is so slight and the stream course so crooked that it is difficult to state accurately the exact position of any of these finds. In no case was the difference in level greater than 15 feet, and in the case of the material not found in place, nothing can be said of its exact position.

DESCRIPTION OF THE FOSSIL VERTEBRATES COLLECTED AT THE BEAVER QUARRY

PISCINE REMAINS

Although the remains of fishes were common at the Cragin Locality, they were much less so at the Beaver Quarry. This may be partly explained by the character of the sediments of the two localities, the former being much

more favorable for the preservation of these delicate fossils. There were a few Ganoid scales found at the Beaver Quarry which are of considerable interest. They are similar to those of the recent *Lepidosteus osseus*, the Mississippi Gar, although on the evidence of scales, specific determination is, of course, not possible. It is of interest that this is the first Pliocene record of this genus although it is recorded from all the other Tertiary epochs.

C. W. Hibbard who was in charge of the field party of the University of Kansas informs me that there were many traces of fossil fishes at this locality. This material was exceedingly fragmentary and was chiefly fin rays, fulcræ and vertebræ. None of it was collected, as it seemed to be indeterminate.

REPTILIA

TESTUDO

An incomplete carapace and plastron of a land tortoise was collected at site 4 in a layer of brown sand. These reptiles are terrestrial forms and inhabit more arid districts. Unfortunately, the specimen is not complete enough to be definitely assigned to one of the many fossil species that have been described in this genus. It is smaller than average forms so far described.

OPHIDIAN

A small procœlus vertebræ, K.U.M.P. No. 3740, which carries well-developed zygosphenes on the anterior end of the pedicle of the neural arch, is reptilian in character. In the details of its construction and in the development of its zygosphenes, it is definitely Ophidian rather than Lacertilian.

MAMMALIA

RODENTIA

Mylagaulus sp.

The genera of the family Mylagaulidæ, as Matthew has shown (1924, 75), are most difficult if not impossible to distinguish on the evidence of

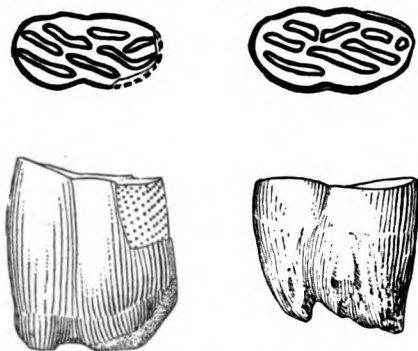


FIG. 3—*Mylagaulus* sp?. Two lower teeth (P4), K.U.M.P. No. 3740, from the Beaver Quarry, Ogallala Lower Pliocene, Beaver County, Oklahoma. Drawn twice natural size by Owen J. Poe.

isolated teeth. Two such teeth, K.U.M.P. Nos. 3740, 3741 (fig. 3), from the Beaver Quarry belong somewhere in this family. They are both P4

and are intermediate in size between the largest and smallest genera of the Mylagaulidæ. In crown pattern, so far as one may determine from the poor figures of the types, these two teeth are similar to *Mylagaulus*, *Epi-gaulus* or *Ceratogaulus*. Matthew also pointed out (1924, 76) that the age variations in the crown pattern of this family is extensive, so it seems impossible at present to carry the identification of individual teeth further than that rank.

CASTORIDÆ

Some of the most important and best-preserved material in this collection is that of a new species of fossil beaver recently described by R. A. Stirton. Occurrences of members of this genus, as fossil, have been recorded throughout the last hundred years. During this time, many genera and species were described, and quite naturally confusion arose as to their interrelationship. This period of analysis of material has but recently been terminated by the publication of Stirton's paper, "A Review of the Tertiary Beavers." In this monograph, Stirton has succeeded in synthesizing the information on this group and showing that, in their phylogenetic sequence and importance in correlation, they exceed in detail all other fossil mammals except the Equidæ.

Eucastor planus Stirton

Referred material—Fragmentary skull, posterior part missing, one incisor present, cheek teeth and palate preserved; complete lower jaw, P1, M1, M3 of left lower jaw, K.U.M.P. No. 3755. This specimen was associated and was chosen by Stirton as the type of the species. Two P4, four lower molars, M1 or M2, one M3 a calcaneum and fragments, all in the University of Kansas Museum.

A palate, No. 32848; three right lower jaws, Nos. 32844, 32845 and 32846; three left lower jaws, Nos. 32842, 32843 and 32847; many teeth and fragments of skeletal elements, all in the University of California Museum of Palæontology.

Description of the material: The following remarks quoted from Stirton's original description (1935, 437) of the species *Eucastor planus* serve to describe the material owned by the University of Kansas:

"The skull is crushed so badly that few cranial characters can be obtained. The palatal foramina opposite M2; central palatal ridge not as prominent as in *E. tortus*; palate wider, and cheek teeth smaller than in *E. tortus* (width between fourth premolars, 4.1 mm., between second molars, 7.7 mm.); P4 with three external striæ; metastris slightly longer than parastris, mesostria longest; M1 in the final S pattern stage; M2 with a hypostria and a mesostria and a metafossette; left M3 with three external striæ and the right M3 with two external striæ and parafossette adjacent to the hypoflexus.

"The right lower jaw is complete, the condyle and angle excepted. It is smaller than any other known species of *Eucastor*. P4 has two internal striids and a tiny metafossettid adjacent to the hypoflexid; M1 and M2 are equal in size and both possess the S pattern; M3 is slightly smaller than M2 and has two internal striids with no metafossettid adjacent to the hypoflexid.

"Isolated lower premolars (P4) in the collection indicate that the internal striids are equal in length, and one P4 shows that there is a short meta-

striid in early stages of wear. The calcaneum does not differ appreciably from that of *E. dividerus*."

The material representing this species obtained by the California party supplements the above description in many points. Stirton has been kind enough to go over this additional material and credit for the following discussion must go to him.

Beside the type, only one other specimen is complete enough to offer characters on the upper dentition. This consists of the interorbital and palatal region of a skull, with the cheek tooth dentition complete and the right incisor present. The teeth are heavily worn; on the left side, P4 shows the base of the parafofsette, hypoflexus deep, mesoflexus deep; metaflexus open to exterior by narrow isthmus. M1 hypofossette and mesofossette present, all other inflections and fossetts absent. M2 hypoflexus and mesofossette present, M1 and M2 equal in size. M3 smaller than other molars and semitriangular in outline, hypoflexus present, mesoflexus opens to exterior by narrow isthmus, metafossette tiny and circular. The cheek teeth of the right side exhibit slight variations in character. P4, parafofsette distinct, mesoflexus deep, opening to the exterior by a narrow isthmus. M1 with hypofossette and mesofossette. M2 about the same size as M1, with hypoflexus and mesofossette. M3 as on the left side, hypoflexus and mesoflexus present, posterior edge of tooth broken away. Width between premolars 3.9; width between M2, 8.8; interorbital width 9.5; postpalatal notch opposite M3; other characters as in the type.

Lower dentition—Six lower jaws of *E. planus*, more or less complete, offer some grounds for weighing characters based on this element. The following descriptions are more detailed than necessary perhaps; but these forms are not yet well understood and the detailed account may be of value in deciding questions of variation and characters in allied forms.

No. 32842; a left lower jaw, ascending ramus, M3, and angle missing. Incisor width, 4.5; mental foramen beneath anterior border of P4. P4, paraflexid strongly curved and anteriorly, mesoflexid relatively short and narrow, hypoflexid deep, mesofossettid absent, hypostriid extends nearly to base of tooth. M1, mesofossettid and hypofossettid present. M2 as in M1, hypoflexid opens to exterior by narrow isthmus indicating base of hypostriid. This is a moderately worn jaw.

No. 32843; a little worn left lower jaw, angle and ascending ramus missing. Incisor 3.5 mm. in width. Tooth pattern of P4 is abnormal in that parafofsettid is present in this stage of wear (paraflexid and parastriid not indicated). Mesoflexid present with mesostriid extending far down the side of the tooth. Metafossettid present but very small; hypoflexid relatively shallow. M1 mesofossettid and hypoflexid present, hypostriid long, extends nearly to base of tooth. M2 small parafofsettid present, mesoflexid opens by shallow groove to lingual side. Hypoflexid and hypostriid present. M3 large parafofsettid, mesoflexid with short mesostriid, no metafossettid, hypoflexid and hypostriid prominent. M3 is as large as other molars in occlusal outline, in contrast to *Eucastor tortus*.

No. 32844; a little worn, right lower jaw, posterior border, angle, and ascending ramus missing. Incisor 4.1 mm. in width. P4 paraflexid strongly curved anteriorly, mesoflexid relatively short, hypoflexid long and narrow, no mesofossettid present. In this last character, this specimen differs from all other little worn P4 from this locality (the rabbit pattern is not present in this early stage of wear). Para and mesostriid long, hypostriid wide. M1 mesoflexid and hypoflexid present, also the accompanying

striids. M2 as in M1, M3 paraflexid shallow with lingual opening, mesoflexid with mesostriid of equal length, hypoflexid with prominent hypostriid. Last molar as large as others.

No. 32845; a large, heavily worn, right lower jaw, angle and ascending ramus missing. Width of incisor 4.0 mm. P4 paraflexid strongly curved anteriorly, short parastriid present, mesoflexid with mesostriid about equal in length to parastriid, metafossettid absent; long sickle-shaped hypoflexid with hypostriid extending to base of tooth. M1 mesofossettid distinct, hypofossettid long, crescentic, extending from lingual to labial borders of the tooth. M2 more heavily worn than M1, hypofossettid shorter than on M1, similar in shape but does not quite extend to lingual border of tooth. M3 worn to point where enamel pattern no longer present.

No. 32846; a moderately worn, right lower jaw, tip of incisor, angle and ascending ramus missing. Incisor 4.2 mm. in width. P4 paraflexid strongly curved anteriorly, mesoflexid short and narrow, parastriid and mesostriid indicated by basal notches, metafossettid absent, hypoflexid long and narrow, hypostriid distinct. M1 mesofossettid and hypofossettid present, no striids. M2 mesoflexid, hypoflexid and hypostriid present. M3 parafofsettid prominent, mesoflexid short, hypoflexid with hypostriid extending to base of tooth. M3 smaller than other molars but more heavily worn.

No. 32847; a heavily worn left lower jaw, incisor, angle and ascending ramus missing. P4 parafofsettid short, straight, mesofossettid one-fourth longer than parafofsettid, no metafossettid present, hypoflexid relatively short, with hypostriid extending to base of tooth. M1 mesofossettid and hypoflexid present, with short hypostriid. M2 as M1, hypostriid represented by basal notch. M3 more heavily worn than other molars, metafofsettid present, hypoflexid extending across the tooth, probably at base of hypostriid, more elongate than M1 or M2.

Remarks—In the heavily worn premolars, the rabbit pattern (parafofsettid) is absent. As indicated in the description of the type, with the exception of No. 32843, the parastriid and mesostriid are equal. The only S pattern present in lower molars is in the type, which has reached just the proper stage of wear to show this. The two species *Eucastor planus* and *E. tortus* are closest to *Dipoides*; but as yet no unquestioned intergradation between the two genera has been found.

CARNIVORA

Bassariscus sp. ?

Referred material—A right lower jaw, angle and ascending ramus missing, P2-3 present, all other teeth missing, U. C. Mus. Pal. No. 32808.

The *Bassariscus*, miner's cat or ring-tailed cat, is a somewhat rare, interesting animal that inhabits the central and western part of North America. Its fossil occurrences are few and are confined to but four species; three of which have been recorded from six localities in the Miocene and Pliocene of North America. This lower jaw from Beaver County (fig. 4) is specifically indeterminate; but it does afford certain characters which suggest that it represents a possible fifth species. It is small; about three-fourths the size of the California representatives of the living species *B. astutus*. It is also smaller than any of the recorded specimens of the fossil species *B. antiquus*, *B. parvis* or *B. ogallalæ*. Unfortunately, the most diagnostic teeth are missing; but P1-3 are in all respects similar to the

living form. The entire dental series measured on the alveoli (P1-M2) is only 25.7 mm. in length and the depth of the ramus beneath P3 is but 5.7 mm.

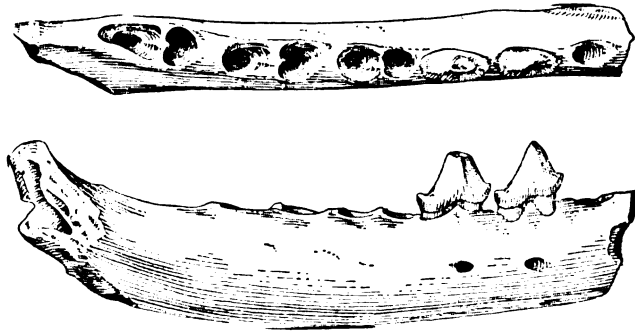


FIG. 4—*Bassariscus* sp?. A right lower jaw, U.C. Mus. Pal. No. 32808, from the Beaver Quarry, Ogallala Lower Pliocene, Beaver County, Oklahoma. Drawn 2.5 times natural size by Owen J. Poe.

Canid indet.

Two incomplete fragments of teeth in the University of Kansas collection must be referred to some small carnivore. The most complete of these two is a deciduous I2, with four well-developed accessory cusps of its posterior (outer) cutting edge. The tooth is small, spatulate, and "saw" like. It is similar to the incisors of *Elurodon platyrhinus*, figured by Barbour and Cook (1917, 178, fig. 4), except this tooth has two cusps of equal development at its tip and two smaller cusps below and to the outer (?) side. The second specimen is the anterior half of the left lower deciduous carnassial of some member of the Canidæ. It is impossible to give a generic determination with certainty on such scanty material.

PERISSODACTYLA

EQUIDÆ

Besides the *Eucastor planus* material described above, the most important elements in the collection from the Beaver Quarry are the equids. Three genera and four species are present in this quarry; but of this lot, only two species are represented by good material. Dozens of species of late Miocene and Pliocene horses have been described; but there seem to be a wide variation of tooth pattern, height of crown, and other characters upon which these "species" are based. It is difficult, if not impossible, to identify specifically an individual tooth, so wide is the variation shown in the type specimens as well as in the material later referred to them. This difficulty is encountered by anyone who attempts to identify a series of teeth. Matthew (1924, 154) was unable to do more than refer the Snake Creek equids to certain "groups" or species, and the same procedure was followed by the writer (1935, 89) in dealing with the horses collected at the type locality of the Ogallala formation. With these points in mind, the Beaver Quarry

equids are placed with the species they most closely resemble, and the solution of the above problem is left for some future revision of the North American species of late Tertiary horses.

Neohipparion

As long ago as 1903, it was suggested (Gidley, 1903, 466) that the North American species referred to the Old World genus *Hipparion* were probably not all members of that genus. Since that time, this concept has been steadily growing, until Gidley's genus *Neohipparion* and Matthew's subgenus *Nannippus* (1926, p. 165) are both given generic rank and many of the species of *Hipparion* are now placed in each of them.

Neohipparion as originally defined (Gidley, 1903, 466) has a relatively larger and more elliptical protocone with the lingual wall flat to concave, simple enamel foldings of the borders of the cement lakes, and (since added by other writers) was a larger form with heavy external ribs. On these characters, there are at least fifteen described species which may be referred to this genus. Within this series of forms, certain groups of species stand out which appear to be closer in their characters to each other than they do to other species which may be referred to the genus.

Matthew (1924, 172) listed four species under the heading "*H. occidentale* group," and at a later time the writer suggested an additional two (Hesse, 1935, 89). The *Neohipparion* specimens collected at the Beaver Quarry are readily referable to this group; but the species is less easily named. Of the group listed by the above writers, the Oklahoma form is probably most closely allied to *Neohipparion coloradense*.

Neohipparion cf. *coloradense* Osborn

Referred material—A premolar, molar and M₃, left side, six lower teeth, No. 3738; a complete series of right lower cheek teeth, P₂ to M₃; and skeletal elements; all in University of Kansas Museum. University of California Museum; left P₄ to M₃, No. 32833; left P₃ to M₁, right M₁₋₃, No. 32834; nine upper teeth No. 32851; right lower jaw, No. 32835; left lower cheek teeth, P₃-M₃, No. 32835; left lower cheek teeth P₃ to M₃, No. 32807; seven lower cheek teeth, No. 32852; incomplete skeletal element.

Description of the material—The Beaver Quarry *Neohipparion* was a moderate sized horse. It was larger than most of the specimens referred to *Nannippus*; but smaller than the majority of the species of *Neohipparion*.



FIG. 5—*Neohipparion* cf. *coloradense*. Upper left P₄ to M₃. U.C. Mus. Pal. No. 32833. Showing typical shape and size of protocones of material collected in the Beaver Quarry, Ogallala Lower Pliocene, Beaver County, Oklahoma. Drawn natural size by Owen J. Poe.

The protocones are elliptical in outline, with rounded, not pointed, anterior and posterior ends (figs. 5, 6a-b). They are approximately three times as long as they are wide and in the premolars are flattened on the lingual side.

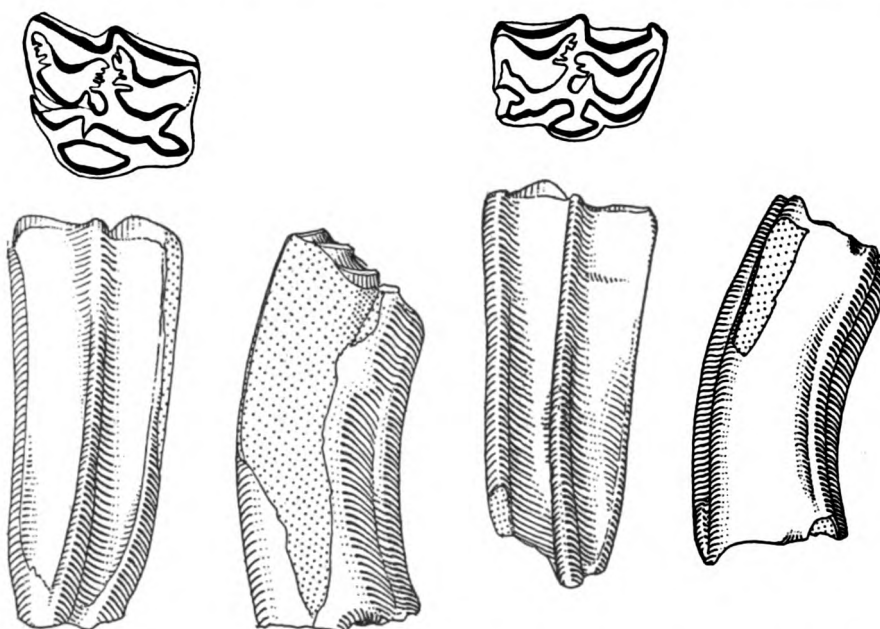


FIG. 6—*Neohipparion* cf. *coloradense*. Two upper teeth K.U.M.P. No. 3738, showing extremes of variation in shape of protocone. Beaver Quarry, Ogallala Lower Pliocene, Beaver County, Oklahoma. Drawn natural size by Owen J. Poe.

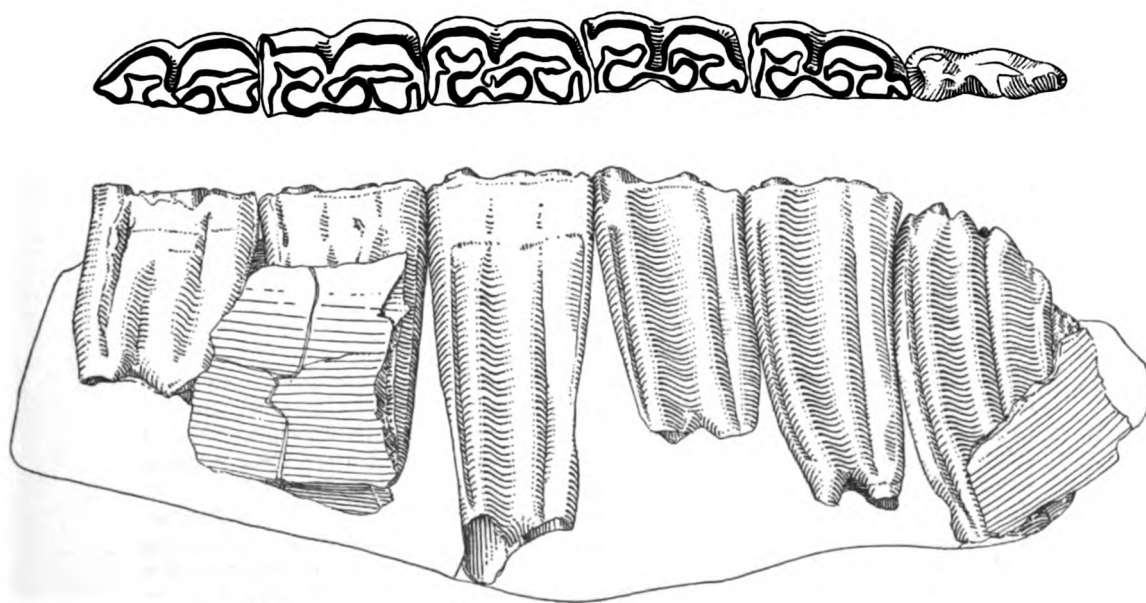


FIG. 7—*Neohipparion* cf. *coloradense*. Left lower jaw, P2-M3, K.U.M.P. No. 3737. From the Beaver Quarry, Ogallala Lower Pliocene, Beaver County, Oklahoma. Drawn natural size by Owen J. Poe.

It resembles most closely the protocone of *N. occidentale*, *N. whitneyi*, *N. dolichops*, or *N. coloradense*. The plication of the borders of the pli-prefossette and pli-postfossette are moderate, about as in *N. occidentale*. The hypoconal groove is widely open in all these teeth, and the hypocone tends to be isolated in many of them. In the majority of the cases, the pli-caballin fold is double, and more rarely single. The external styles are not as heavy as in the other species of *Neohipparion*.

Lower dentition—The lower teeth (fig. 7) are typically *Hipparion*-like. They are slightly smaller than the lower teeth of the other species of *Neohipparion*. The metaconid and metastylid are rounded and separated by a shallow trough which extends to the base of the tooth. Some variation is shown in this character, in general, the valley between the two styles is more marked in the molars, while in the premolars it is often almost flat. The styles do *not* tend to become flattened or elongate. The protoconid and hypoconid are somewhat flattened (on the buccal side) in the premolar teeth, and the valley between the two is especially deep in the molar teeth, often nearly meeting that of the metaconid-metastylid.

RELATIONSHIP OF THE BEAVER QUARRY NEOHIPPARIONS

On the basis of size, height of crown, shape of protocone, and complication of enamel folds, the Oklahoma *Neohipparion* may be referable to *N. coloradense*; but that form is based upon such fragmentary material that definite reference is out of the question. The Oklahoma form is smaller than any other member of the "*H. occidentale* group" of Matthew, although it resembles closely several species of it.

Nannippus sp?

Referred material—Eight upper and six lower teeth in University of Kansas Museum, Nos. 3736-3738; two upper and eleven lower teeth in University of California Museum, No. 32853.

Unfortunately, this interesting and important little equid can not at this time be given specific reference. The above individual teeth seem to represent an unrecognized species of the genus *Nannippus*. They are moderately high-crowned and smaller than any known species of the "*Hipparion*" group except *Nannippus minor*. The external styles are prominent but not heavy, and the enamel borders of the cement lakes show little complication. The protocone is oval in outline, prominent and is narrowly joined to the protoloph in many of the worn teeth. The hypoconal groove, when present, is an isolated lake in both worn and unworn teeth. Certain individual teeth, taken alone, might readily be called *Protohippus* (as it has been defined); but the entire series belongs, apparently, in *Nannippus*. In some respects, these teeth are close to the figured types of Leidy's *N. gratum* (1869, pl. XVIII, figs. 25-30); but they are distinctly smaller than those of Gidley's neotype (Osborn, 1918, 180, figs. 142-143), of the latter species. In the University of California collections made at the Clarendon zone, there are many isolated teeth, jaws and maxillaries of this small *Nannippus*. The Clarendon specimens show fewer cases of the protocone connecting with the protoloph, a fact which may be interpreted as indicative of a slightly more primitive character on the part of the Beaver Quarry specimens.

The lower teeth have a small triturating surface, are moderately high-crowned (averaging three times the anterior-posterior length), and have

rounded metaconids and metastylids. The valley separating these two is deep and V shaped, distinct from crown to base.

This small species of *Nannippus* is an important one in the correlation of the Lower Pliocene faunas of the southern Great Plains. It is, apparently, the counterpart of *N. gratum* of the north, although it may be slightly younger than that form. Its thorough description and specific designation must be left for a later time when a better type and more adequate material may be studied.

Calippus martini

Referred material—University of Kansas; individual teeth, uppers, No. 37; University of California; left cheek teeth P₃ to M₃, No. 32836; right cheek teeth P₄–M₃, No. 32836; and probable skeletal elements.

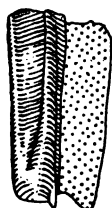
The above specimens do not add to the description of this species given under the discussion of the Cragin locality. They do prove that this form was present in both localities with no appreciable difference in structure.

Calippus sp. ?

A single upper tooth (fig. 8) of a very small horse also seems to be referable to the above genus. The tooth is, in all proportions, smaller than any described species of late Tertiary horses unless it be comparable with



FIG. 8—*Calippus* sp?. An upper tooth, K.U.M.P. from the Pliocene of Beaver County, Oklahoma. Drawn natural size by Owen J. Poe.



Nannippus minor. There are several teeth of this tiny equid in the collections made in the Clarendon zone (in U. C. Mus. Pal.); but they have not yet been described. The crown of this tooth is almost square (13×12 mm.) and it is moderately hypsodont. The protocone is narrowly joined to the protoloph, the cement lakes are large with simple, non-folded borders, and the mesostyle is sharp and prominent but flares into a heavy rib toward the base of the tooth. In comparison with the described species of both *Calippus* and *Protohippus*, this small tooth exhibits the characters of both. It resembles most closely *Calippus placidus*, but is slightly smaller than that form.

ARTIODACTYLA

Prosthennops sp. ?

The genus *Prosthennops* is represented in the University of Kansas collection by a large, moderately worn M₃. Unfortunately, this tooth is not clearly diagnostic of the species of this genus. It is a large tooth

(13.5×26.8), with four prominent, main cusps on the anterior half, and a well-developed triangular heel with several small cusps making up the posterior half. In so far as this tooth may be specifically determined, it is a member of the *P. crassigenis*-*P. serus* group, and in size is nearer the latter species. A second specimen referred to this genus is an ungual phalanx, which corresponds in size and construction to the ungual phalanges of both fossil and recent peccaries in this Museum.

? OREODONTINÆ

A fragment of the left lower jaw with dp3-4, belongs to some genus of the above subfamily. It is not one of the larger Pliocene forms such as *Pronomotherium*, but would correspond in size with *Merychys* or *Metoreodon*. Two metacarpals in this collection resemble closely similar elements in the foot of an oreodon, with which they are placed; although it is possible that they represent *Prosthennops*.

CERVIDÆ

The astragalus of a small artiodactyl is probably referable to the genus *Blastomeryx*. This specimen, K.U.M.P. No. 3739, is small; but does not differ in any important detail from similar skeletal elements of either *Blastomeryx* or *Merycodus*. It is smaller than the astragalus of any merycodont with which it could be compared; but is very close in size to the

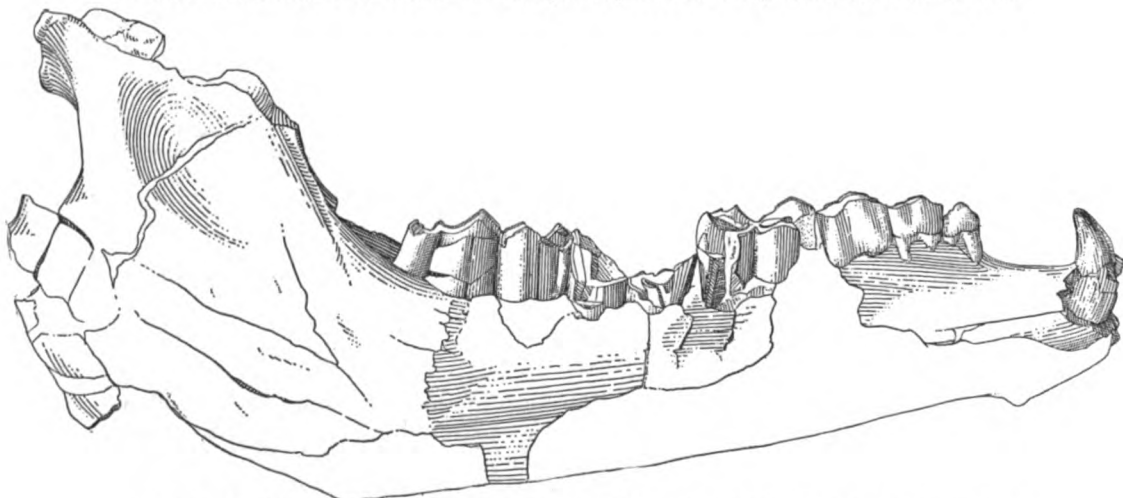


FIG. 9.—? *Alticamelus*. Right lower jaw, PI to M3, U.C. Mus. Pal. No. 32855. From the Beaver Quarry, Ogallala Lower Pliocene, Beaver County, Oklahoma. Drawn one half natural size by Owen J. Poe.

average species of *Blastomeryx*. This latter genus is predominately Miocene; but several species have been recorded from the Pliocene (Matthew, 1924, 195).

CAMELIDÆ

? *Alticamelus*

Referred material—University of Kansas; symphysis of a lower jaw, dp 3-4, No. 3784, two teeth. University of California; right lower jaw from Site 4, PI to M3; No. 32855; teeth and fragments.

The remains of fossil camels are generally common throughout the later Tertiary deposits of the High Plains. The entire collection made in Beaver County was an exception to this, since few camelids were found there. The best specimen of the lot (fig. 9), a right lower jaw, is not well preserved, but seems to offer sufficient characters for generic determination. The dentition is complete, the diastema between $P1$ and $P2$ short (25.0), $P2$ double-rooted and large, $P3$ elongate with a triangular crown, $P4$ blade-like, but much more molariform than $P3$. The molars are badly battered but were high-crowned and large. The dental series is long ($P2-M3$, 153.0). The caniniform $P1$ is not heavy and tends toward a blade rather than a conical tooth. The jaw does not have the slender proportions of a *Procamelus* in spite of certain characters which resemble that genus.

CORRELATION OF THE FOSSIL VERTEBRATES FROM THE OGALLALA FORMATION (LAVERN ZONE) OF BEAVER COUNTY, OKLAHOMA

The fauna described in the foregoing pages is in many respects very incomplete. Most of the forms which may be identified can be given no more than a generic reference. Nevertheless, certain forms offer a basis for correlating the assemblage with others that have been described from North America.

So far as I am able to determine, the material described from the various localities in the Beaver area represents but one fauna. Although it is distributed throughout many feet stratigraphically, there is no apparent change in comparable forms from the bottom to the top. The entire assemblage was collected, *in situ*, at various localities below the horizontal "Biorbia zone" of Elias, in the deformed strata referred to as the "Lavern zone" by Waite. Therefore, until further collecting shows this conclusion to be in error, the fossils of the Beaver area are regarded as a unit fauna and are treated as such in this discussion.

The fossil beaver, *Eucastor planus*, and the fossil horses give an excellent basis for placing a definite age on this assemblage as well as showing something of its relationships to other faunas. Species of the genus *Eucastor* have been recorded in the following faunas: Esmeralda, Nevada; Orinda-Siesta, California; Little White River and Big Springs Canyon, South Dakota. The species *E. planus* is, of course, confined to this locality in Oklahoma. The genus is then one that occurs (so far as we know at present) in the older Pliocene since each of the above listed finds carry material of that type. Of the fossil equids, *N. coloradense* is recorded from only one other locality, the upper Pawnee Creek fauna of northeastern Colorado. The species of *Nannippus* referred to above as probably new is, so far as I am aware, confined to the Beaver, Oklahoma, locality and the Clarendon of Texas. The same is true of the exceedingly small *Calippus*. The remaining elements of the fauna are in no case advanced, but must be regarded as fairly primitive in comparison to other faunas of the Pliocene.

From this evidence, it seems apparent that the Beaver fauna is most closely related to the Clarendon of Texas (fig. 10, No. 12) and more distantly to the Esmeralda, Big Springs Canyon, Burge (Stirton and McGrew, 1935, 129) and other faunas of Lower Pliocene age. Unfortunately, the subdivisions of the Pliocene of North America are not well defined in print.¹ The faunas mentioned above are the most primitive of those referred to that epoch and are, therefore, called Lower Pliocene. They are not to be confused with the faunas which carry high-crowned equid teeth, advanced species of *Dipoides*, and diversified Artiodactyla. Many of these more advanced types of fauna, as pointed out in the introduction of this report, have been called Lower Pliocene because of the confusion of much of the early work.

The whole question of the correlation of the North American Lower Pliocene with that of China, India and Europe is most difficult to discuss. In general, the Hipparions of the Old World, from faunas that are called Lower Pliocene, appear to be more advanced than those of this country. The Pikermi and Samos, generally regarded as Pontian in age, are believed by many to be Upper Miocene, yet the Hipparions of these faunas are certainly advanced over those discussed in this report. It is possible that some confusion exists in the Old World, as it did in this country 25 years ago, concerning the interrelationships of the "Pontian" faunas. Perhaps several stages of the Pliocene exist there and have been, thus far, unrecognized.²

¹This task has recently been completed by Mr. R. A. Stirton, whose paper will appear in the American Journal of Science some time during 1936-37. To Mr. Stirton, and his manuscript, the writer is indebted for much valuable information on the correlation of the high plains faunas.

²At the time of writing the above paragraph, I note the publication of Dr. Edwin H. Colbert's "Siwalik Mammals in the American Museum of Natural History," which I have not yet seen. Judging from the table of contents (Science, n.s., 83, No. 2146, p. 2), many important questions involving the Siwalik faunas are discussed. It is only by such exhaustive treatises as this appears to be that the correlation problems of the New and Old World will be solved.

KEY TO FIGURE 10

1. *Feldt Ranch Fauna*, Middle Pliocene, Keith County, Nebraska.
2. "*Republican River Fauna*," not a unit fauna, collected at many localities, seems to represent Miocene, Lower and Middle Pliocene, Kansas and Nebraska.
3. *Edson Fauna*, Middle Pliocene, Sherman County, Kansas.
4. *Rhinoceros Hill Fauna*, Middle Pliocene, Wallace County, Kansas.
5. *Collins Draw Fauna*, Middle Pliocene, Wallace County, Kansas.
6. *Wray* or "*Beecher Island*" *Fauna*, Middle Pliocene, Yuma County, Colorado.
7. *Optima Fauna*, Middle Pliocene, Texas County, Oklahoma.
8. *Beaver Fauna*, Lower Pliocene, Beaver County, Oklahoma.
9. *Hopewell Fauna*, Pliocene, Ellis County, Oklahoma.
10. *Higgins Fauna*, ?Middle Pliocene, Lipscomb County, Texas.
11. *Hemphill Fauna*, Middle Pliocene, Hemphill County, Texas.
12. *Clarendon Fauna*, Lower Pliocene, Donley County, Texas.
13. *Blanco Fauna*, Upper Pliocene, Crosby County, Texas.



FIG. 10—Shaded area represents distribution of Ogallala formation over High Plains, areas of uncertain relations indicated by question marks and dotted lines. Arrows and numbers show approximate position of the faunas recorded from this formation.

ENVIRONMENTAL CONDITIONS SUGGESTED BY THE
VERTEBRATE FAUNA

There can be no question of the fact that plants, such as those collected in Beaver County, are much better climatic indicators than the vertebrates. The ecologic conditions under which this flora lived have been described by Chaney and Elias. Obviously, the same general conditions would apply for the vertebrates of this area, but since they were more widely ranging they add to the evidence of the plants in several important respects.

So far as I am able to determine, the vertebrate fauna may be divided into the following groups on the basis of their probable habitats.

1. The perch and gar-pike fishes were, of course, inhabitants of the stream itself. In this same region today these fishes still exist. The beavers too are indicative of permanent streams, although not confined to them.

2. Probably the best vertebrate form representing a stream valley habitat is the beaver. Although its descendants are extinct in this region today they ranged over this area within the last few years. *Bassariscus* is usually found in brushy or rocky areas near streams. It may be regarded as typical of the environment indicated by the flora. The fossil peccary and the cervid-like *Blastomeryx* are probably assignable to the stream-border. The modern representatives of these genera are all inhabitants of brushy or wooded areas.

3. The horses of the Beaver Oklahoma fauna are considered as indicative of the open upland away from the streams, since their adaptations are along that line. *Hipparion* (*Neohipparion* and *Nannippus*) has been spoken of as the "Desert Horse" (Osborn, 1905, 7, and others)—an assumption based on the idea that retention of the lateral digits is indicative of life on sandy ground. I know of no way in which this observation may be substantiated, and it seems to be mentioned with less frequency in the literature of more recent years. The *Hipparion* group occurs commonly in the great plains faunas in association with monodactyl forms which are regarded as normally those of an open country. One can say but little of the habits of the *Oreodon*. A herd habit, as indicated by their abundance and their fossil occurrence in groups, suggests that they were inhabitants of the more open country. The rhinoceros, today, seems to represent a savannah habitat, transitional between the valley and upland types.

It would appear from the accounts of the undisturbed animal life of the great plains that the wooded stream borders were a meeting place for both the upland and forest-dwelling animals. One might therefore expect just such a mixed assemblage of plains and valley mammals as occur in the Beaver fauna, in association with fossil plants of a flood-plain type. In age and in environmental conditions the evidence of the fossil animals and plants is in complete accord.

The idea that most of the vertebrate faunas of the High Plains represent accumulations at watering places has been expressed by many writers, and so far as one can determine this is borne out by the evidence in most cases. Usually the upland elements of the fauna are more common and hence receive the most emphasis. The smaller, less common, forest types are less frequently preserved, or are not given much weight in considering the environmental picture of the fauna as a whole. Unfortunately, too, fossil plants such as those from Beaver are rarely associated with the vertebrate faunas. Without them, and with only the vertebrate faunas as guides, there would be no indication of the minute differences of environment that Chaney and Elias have been able to point out.

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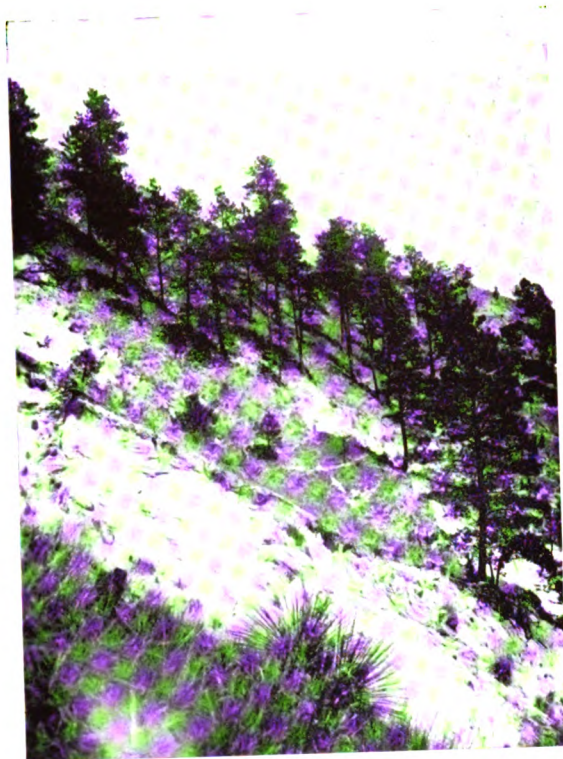


FIG. 1—White Cliffs locality on Plum Creek, northwestern Brown County, Nebraska.

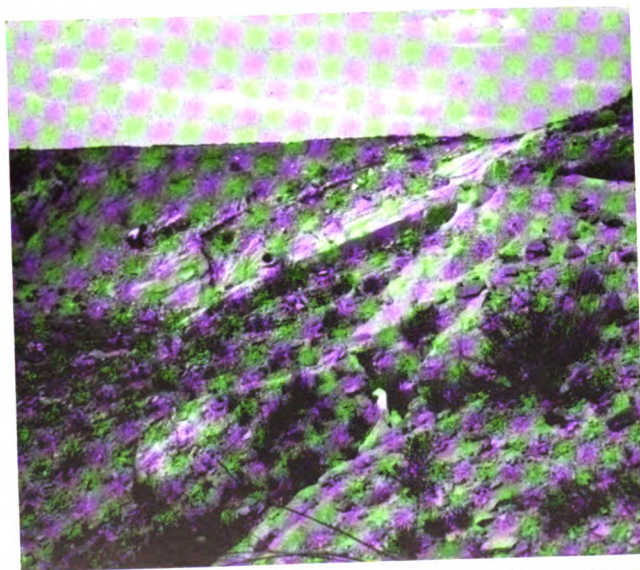


FIG. 2—Fossil locality in diatomaceous marl, Beaver County, Oklahoma.

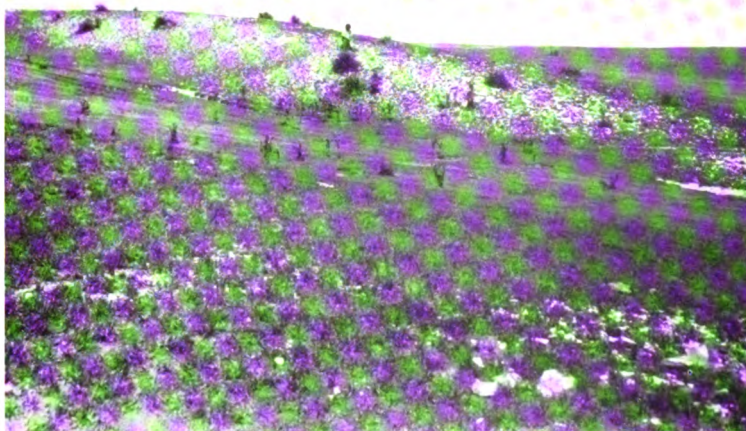


FIG. 1—Leaf locality in flint, overlying diatomaceous marl, Beaver County, Oklahoma.



FIG. 2—Valley of Canadian River, south of Oklahoma City, Oklahoma, showing flood-plain vegetation. (Photograph by E. S. Clements.)



FIG. 1—Diatomaceous marl in northeastern Wallace County, Kansas, near the Logan County fossil locality.



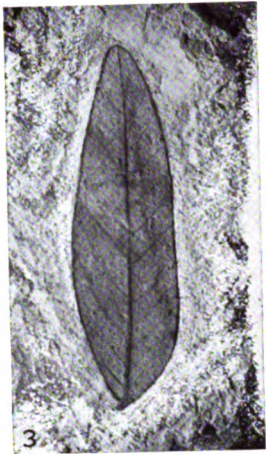
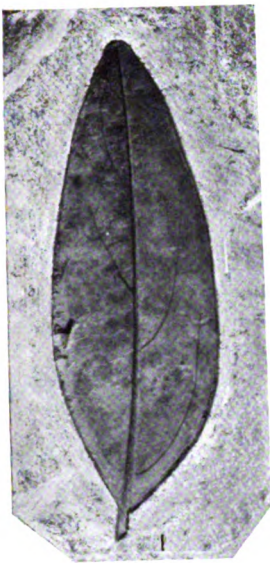
FIG. 2—Valley, South Fork of Arkansas River, east of Tonkawa, Oklahoma, showing floodplain vegetation.

PLATE 4

FIGS. 1, 3, 6—*Salix coalingensis* Dorf. Plesiotypes. Localities P-42, P-43, P-44. U. S. Nat. Mus. Nos. 39336, 39337, 39338.

FIG. 2—*Cyperacites* sp. x4. Plesiotype. Locality P-42. U. S. Nat Mus. No. 39333.

FIGS. 4, 5—*Populus lamottei* Chaney and Elias. Cotypes. Locality P-44. U. S. Nat. Mus. Nos. 39334, 39335.



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PLATE 5

FIGS. 1, 3—*Celtis kansana* Chaney and Elias. Cotypes. Locality P-42. U. S. Nat. Mus. Nos. 39339, 39341.

FIG. 2—*Celtis kansana* Chaney and Elias. Endocarp. Cotype. Locality P-43. U. S. Nat. Mus. No. 39340.

FIGS. 4, 5—*Celtis kansana* Chaney and Elias. Cotypes. Locality P-43. U. S. Nat. Mus. Nos. 39342, 39343.

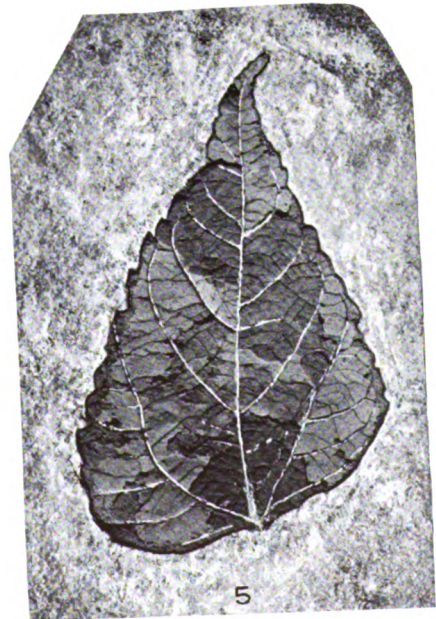


PLATE 6

FIG. 1—*Ulmus moorei* Chaney and Elias. Holotype. U. S. Nat. Mus. No. 39344.

FIGS. 2-5—*Ulmus moorei* Chaney and Elias. Paratypes. Localities P-42, P-43. U. S. Nat. Mus. Nos. 39345-39348.

FIG. 6—*Bumelia florissanti* Lesquereux. Plesiotype. Locality P-44. U. S. Nat. Mus. No. 39358.

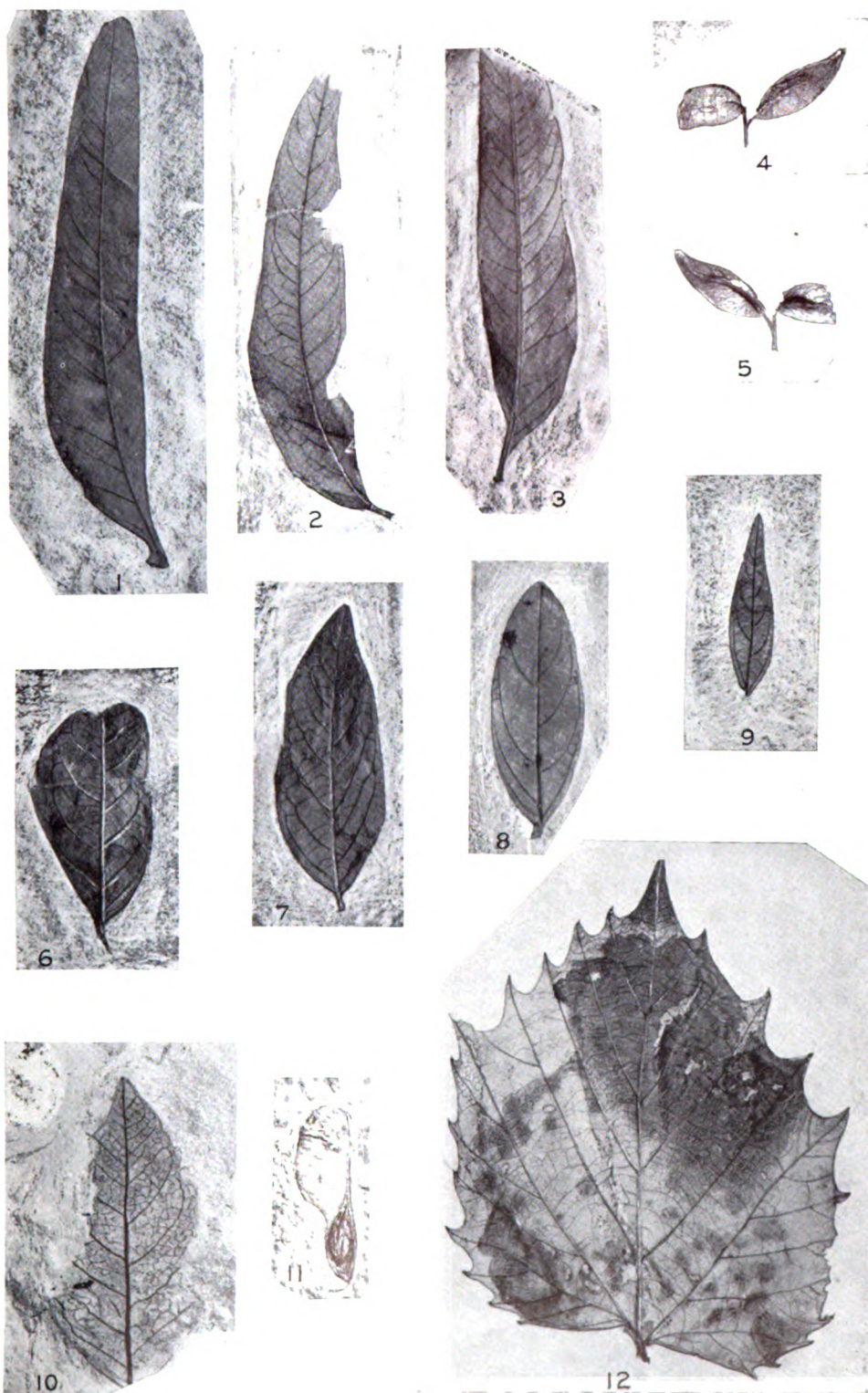
FIG. 7—*Gymnocladus casei* Berry. Plesiotype. Locality P-42. U. S. Nat. Mus. No. 39352.

FIGS. 8-10—*Frazinus ungeri* Lesquereux. Plesiotypes. Locality P-42. U. S. Nat. Mus. Nos. 39362-39364.



PLATE 7

- FIGS. 1, 3**—*Sapindus oklahomensis* Berry. Plesiotypes. Localities P-42, P-44. U. S. Nat. Mus. Nos. 39355-39357.
- FIGS. 4, 5**—*Cercidiphyllum crenatum* (Unger) R. W. Brown. Follicles. (Figure 5 is counterpart of figure 4.) Plesiotypes. Locality P-44. U. S. Nat. Mus. Nos. 39350a, 39350b.
- FIGS. 6-8**—*Diospyros preterana* Chaney and Elias. Cotypes. Localities P-42, P-44. U. S. Nat. Mus. Nos. 39359-39361.
- FIG. 9**—*Phyllites* sp. Holotype. Locality P-44. U. S. Nat. Mus. No. 39365.
- FIGS. 10, 11**—*Acer negundoides* MacGinitie. Plesiotypes. Locality P-44. U. S. Nat. Mus. Nos. 39353, 39354.
- FIG. 12**—*Platanus aceroides* Göppert. Plesiotype. Locality P-44. U. S. Nat. Mus. No. 39351.



CONTRIBUTIONS TO PALÆONTOLOGY

II

**A LATE TERTIARY FLORA FROM
SOUTHWESTERN IDAHO**

By ERLING DORF

With three plates and two text-figures

[Issued November 20, 1936]

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A LATE TERTIARY FLORA FROM SOUTHWESTERN IDAHO

INTRODUCTION

Although fossil plants have long been known from the Payette formation,¹ which is interbedded with the extensive Columbia River basalt in southwestern Idaho, no plant material has been secured until recently from the sediments which definitely overlie the basalt. Collections made by the writer from such sediments have now yielded a flora of 45 species. It is the purpose of this paper to describe the occurrence and composition of this flora and to discuss its climatological and stratigraphic significance.

Collections were made with the assistance of Freeman Foote and John H. Coulter during two weeks of the 1930 field season, under the joint auspices of Carnegie Institution of Washington and Princeton University. The project was undertaken at the suggestion of Dr. Ralph W. Chaney and Dr. Virgil R. D. Kirkham.

The geology of southwestern Idaho has been ably discussed from both the stratigraphic and palæontologic points of view by a large number of authors including Lindgren,² Merriam,³ Buwalda,⁴ Kirkham,⁵ Renick,⁶ Anderson⁷ and Stearns.⁸ Kirkham gives an excellent historical summary of ideas regarding the stratigraphy and geologic history of this region. He also includes a list of 21 forms of fossil plants obtained from the sediments above the Columbia River basalt. These were tentatively identified by Berry, who recognized only 11 species which could be specifically determined. The larger collections obtained by the writer since then have more than doubled the number of forms and have made possible a greater number of specific determinations.

The writer gratefully acknowledges the critical interest and encouragement of Dr. Ralph W. Chaney. Friendly cooperation has been given by members of the staff of The New York Botanical Garden and by Dr. Virgil R. D. Kirkham.

GEOGRAPHIC AND GEOLOGIC OCCURRENCE

Collections have been made by the writer from four localities, all of which lie within a radius of 20 miles of the town of Weiser, Idaho. Weiser is situated on the Snake River of southwestern Idaho in Sections 32 and 33,

¹ Knowlton, U. S. Geol. Surv., Eighteenth Ann. Rept. pt. 2, 721-744, 1898; Chaney, Amer. Jour. Sci., 5th ser., vol. 4, 214-222, 1922.

² Lindgren, U. S. Geol. Surv., Eighteenth Ann. Rept. pt. 3, 625-736, 1898.

³ Merriam, Univ. Calif. Dept. Geol. Bull., vol. 10, 421-443, 1917.

⁴ Buwalda, Idaho Bur. Mines and Geol. Pamph. 5, 1923.

⁵ Kirkham, Jour. Geol., vol. 39, No. 3, 193-239, 1931.

⁶ Renick, Jour. Geol., vol. 38, No. 6, 509, 1930.

⁷ Anderson, Idaho Bur. Mines and Geol. Pamph. 41, 1934.

⁸ Stearns, U. S. Geol. Surv. Water Supply Paper, Manuscript.

Township 11 North, Range 5 West. All but one of the localities are included in the area covered by the Weiser Reconnaissance Map of the United States Geological Survey. The distribution of the four localities listed below is shown in figure 1.

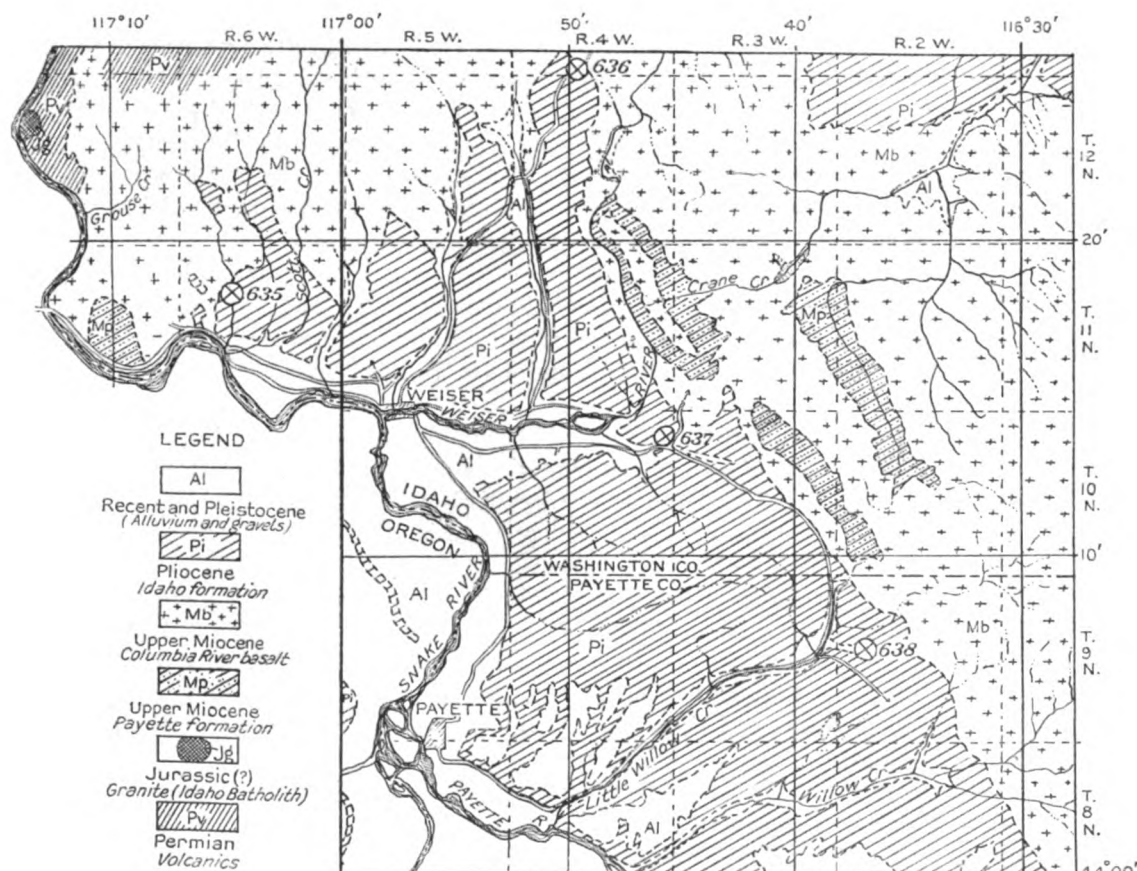


FIG. 1—Geologic Map of the Weiser area, showing location of the four plant localities. (Adapted from Kirkham, Jour. Geol., vol. 39, No. 3, fig. 13, 1931.)

Locality No. 635: West Bank of Hog Creek, southeastern quarter of Section 8, Township 11 North, Range 6 West, 9.2 miles North 55° West of Weiser, Idaho. Plant impressions occur in thinly bedded, cream-colored, soft shales, less than 150 feet above the Columbia River basalt.

Locality No. 636: Road cut on North and South Highway, southwestern quarter of Section 33, Township 13 North, Range 4 West, 14.2 miles North 30° East of Weiser. Plants occur in thickly bedded white tuffs, less than 100 feet above the basalt.

Locality No. 637: North side of Cove Creek, northeastern quarter of Section 12, Township 10 North, Range 4 West, 10 miles East 5° South of Weiser. Plants occur in massive, irregularly bedded, coarse, white tuffaceous sandstones, less than 350 feet above the basalt.

Locality No. 638: North bank of Alkali Creek, northeastern quarter of Section 17, Township 9 North, Range 2 West, 19 miles East 26° South of Weiser. Plants occur in creamy white, diatomaceous shales and in thinly bedded coarse, gray sandstone, about 1000 feet above the basalt.

The sediments from which the plant remains were obtained lie discontinuously on the upper series of the Columbia River basalt, which in turn overlies about 600 feet of indurated shales of the Payette formation. The stratigraphic position of the plant-bearing horizons is indicated in the generalized columnar section shown in figure 2. The strata from which plants were collected, comprising the first thousand feet of beds above the upper basalt, were originally included in the Miocene Payette formation by Lindgren.¹ At a later date, they were defined as the Poison Creek formation by Buwalda,² who assigned a lower Pliocene or later age to them on the basis of mammalian remains. Buwalda separated the Poison Creek formation from the overlying Idaho formation by a slight angular unconformity. In a subsequent report on the Weiser area, Kirkham³ retained the name Poison Creek formation for the beds and defined the overlying beds as the

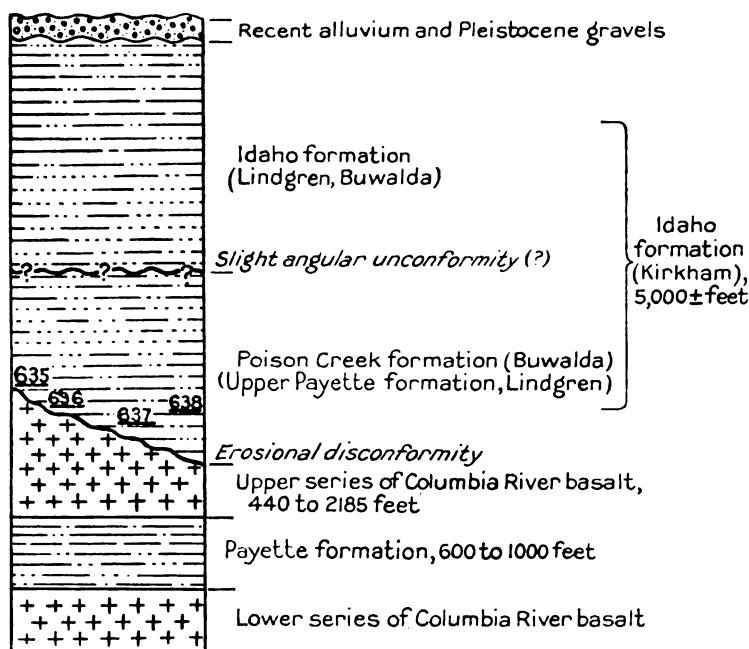


FIG. 2—Generalized columnar section in the Weiser region, showing approximate position of plant-bearing horizons at the four localities. (Adapted from Kirkham, Jour. Geol., vol. 39, 193-239, 1931).

Emmett formation. On the basis of more extensive field work in the area. Kirkham⁴ has recently included the plant-bearing beds as well as the overlying beds in the Idaho formation. Evidence for the slight angular unconformity between the lower and upper members of the formation is consid-

¹ Lindgren, U. S. Geol. Surv. Eighteenth Ann. Rept. pt. 3, 623-637, 1898.

² Buwalda, *op. cit.*

³ Kirkham, Idaho Bur. Mines and Geol., Pamph. 29, 1928.

⁴ Kirkham, Jour. Geol., vol. 39, No. 3, 193, 1931.

ered lacking by Kirkham, who explains apparent slight differences in dip as due to "continuous deposition in a progressively sinking area."¹ The Payette formation is shown by Kirkham to be lithologically, stratigraphically and palæontologically distinct from the Idaho formation.

The relation of the plant-bearing beds (whether they be considered upper Payette, Poison Creek, or Idaho formation) to the underlying Payette formation is of considerable significance. In the Weiser area the Payette is clearly separated from the overlying plant-bearing beds by at least one erosional unconformity and by a thickness of 440 to 2185 feet of basalt. South of the Weiser area, there is an additional series of lavas, the Owyhee rhyolite, which intervenes between the upper basalt and the overlying plant-bearing beds. These relationships and their implications in terms of elapsed geologic time are extremely significant to the discussion of the age of the plant-bearing beds of the Weiser area.

From the stratigraphic relationships of the various lavas and sediments, it is difficult to determine the altitudinal limits within which the plant-bearing beds were deposited. The outcrops from which the writer's collections were made occur at elevations of from 2500 to 3200 feet above sea-level. There is evidence, however, that downwarping has occurred in parts of the region, particularly in the central portion of the depositional basin. From well logs at Ontario, Payette, and Weiser, for example, it is apparent that the upper series of the Columbia River basalt, which underlies the plant-bearing beds, has not been penetrated at depths of 1839 feet below sea-level, 352 feet and 629 feet above sea-level respectively.² On the other hand, the upward arching of the Columbia River basalt in the Blue Mountains to the northwest of Weiser,³ the occurrence of Columbia River basalt lying on granite at elevations of 7200 feet to the east,⁴ and the remnants of Payette beds at elevations of from 4600 to 6900 feet to the southeast⁵ indicate that uplift occurred in contiguous areas. Unfortunately, the plant-bearing outcrops lie along the edge of the basin where the evidence for either uplift or depression is not clearly shown. Hence it can only be inferred that the sediments were laid down at medium elevations, probably 2000 to 4000 feet above sea-level.

PRESENT PHYSICAL CONDITIONS AND VEGETATION

The Weiser area lies within the Snake River Plains which border the level flood-plains and terraces of the Snake River. The topography of the plains is maturely dissected with irregular, linear ridges rising 500 to 700 feet above the general level, which stands at about 2200 to 2800 feet above sea-level. The broad, flat flood-plains and terraces of the Snake River and

¹ Kirkham, *op. cit.*, page 205.

² Kirkham, *Jour. Geol.*, vol. 39, 237, 1931.

³ Fenneman, *Physiography of Western United States*, 232, 1931.

⁴ Kirkham, *Jour. Geol.*, vol. 38, 652, 1930.

⁵ Lindgren, *U. S. Geol. Surv., Nampa Folio*, No. 103, 1, 1904.

the lower portions of its larger tributaries are developed at elevations of about 2100 to 2200 feet. The general level of the plains rises gradually within 50 miles toward the east, north, and south to the higher levels of the Boise Mountains, the Blue Mountains, and the Owyhee Range, respectively.

Climatically the Weiser area is in the cool arid province on the basis of moisture and temperature conditions.¹ The normal annual precipitation averages between 10 and 13 inches, most of which falls during the months from October to May. During the average frostless season, which normally lasts for about 140 days between the middle of May and the end of September, there is usually only between 3 and 7 inches of rainfall. The normal mean annual temperature averages about 50°F. Extreme temperatures of over 100°F. and below -20°F. are infrequent. The normal mean temperature for the major portion of the year is between 32°F. and 68°F., with about 72 days of the remainder of the year averaging above 68°F., and about 56 days below 32°F.

The vegetation of the area is characteristically of the Upper Sonoran life-zone,² which in this region is dominated by the *Atriplex-Artemisia* association of the Basin Sagebrush Formation.³ The common black sage *Artemisia tridentata* Nutt., the winter-fat *Eurotia lanata* (Pursh) Moq., the salt-bush, *Atriplex confertifolia* Wats., and the rabbit brush, *Chrysothamnus nausosus* (Pall.) Britton are the more abundant species of the xeric prairie shrubs. Less common are the greasewood, *Sarcobatus vermiculatus* (Hook.) Torrey, which is restricted to the more alkaline soils, and the hop sage, *Grayia spinosa* (Hook.) Moq., and antelope brush, *Purshia tridentata* DC., which occur sparingly on the higher ridges. Patches of bunch grass, presumably *Agropyron spicatum* (Pursh) Scribn. & Sm., and blue grass, *Poa* spp., are not infrequent at higher elevations.

In the arid plains there is no native tree growth to relieve the monotony of the sparse covering of small shrubs and grasses. Along the permanent streams, however, several species of trees are a pleasant fringe in the landscape. *Populus tremuloides* Michx., *P. trichocarpa* Torr. and Gray, *Alnus tenuifolia* Nutt., and several species of *Salix* are the most prominent, usually in association with a number of shrubs, such as *Betula fontinalis* Sarg., *Ribes inerme* Rybd., *Prunus demissa* (Nutt.) Dietr., *Amelanchier alnifolia* Nutt., *Crataegus* spp., and *Rosa* spp. These species increase in abundance and additional forms appear in the higher, more mesic forests within 50 miles east and northwest of the Weiser area where the yellow pine forest, dominated by *Pinus ponderosa* Dougl., *P. contorta* var. *latifolia* S. Wats., and *Pseudotsuga taxifolia* Britt., indicates the change from the upper Sonoran to the Transition zone.

¹All climatological data has been taken from the excellent maps, tables and summaries in Livingston and Shreve, *Distribution of Vegetation in the United States as related to Climatic Conditions*, Carnegie Inst. Wash. Pub. No. 284, 1921.

²Livingston and Shreve, Carnegie Inst. Wash. Pub. No. 284, pl. 73, 1921.

³Clements, Carnegie Inst. Wash. Pub. No. 290, 156-160, 1920.

COMPOSITION OF THE FLORA

The Weiser flora is made up of 45 species which represent 32 genera and 23 families. The large majority of the species, namely 31, are dicotyledons; in the remaining number there are 10 conifers, 2 monocotyledons, 1 fern, and 1 horse-tail.

SYSTEMATIC LIST OF SPECIES

Pteridophyta	Fagaceæ
Polypodiales	<i>Castanopsis convexa</i>
Polypodiaceæ	<i>Quercus browni</i>
<i>Dryopteris idahoensis</i>	<i>Quercus cognata</i>
Equisetales	<i>Quercus declinata</i>
Equisetaceæ	<i>Quercus duriuscula</i>
<i>Equisetum</i> sp.	<i>Quercus mccanni</i>
Spermatophyta	<i>Quercus simulata</i>
Coniferales	Ulmaceæ
Pinaceæ	<i>Ulmus moorei</i>
<i>Pinus knowltoni</i>	<i>Ulmus speciosa</i>
<i>Pinus tetrafolia</i>	Platanaceæ
<i>Pinus</i> sp.	<i>Platanus dissecta</i>
<i>Picea lahontense</i>	Cercidiphyllaceæ
<i>Pseudotsuga masoni</i>	<i>Cercidiphyllum crenatum</i>
<i>Abies</i> sp.	Berberidaceæ
Taxodiaceæ	<i>Odostemon simplex</i>
<i>Sequoia langsdorffii</i>	Rosaceæ
Cupressaceæ	<i>Prunus rustii</i>
<i>Libocedrus</i> sp.	<i>Cercocarpus antiquus</i>
<i>Thuja garmani</i>	Leguminosæ
<i>Juniperus sabinoides</i>	<i>Leguminosites</i> sp.
Monocotyledonæ	Rutaceæ
Typhaceæ	<i>Ptelea miocenica</i>
<i>Typha lesquereuxi</i>	Celastraceæ
Cyperaceæ	<i>Celastrus</i> sp.
<i>Cyperacites</i> sp.	Aceraceæ
Dicotyledonæ	<i>Acer chaneyi</i>
Salicaceæ	<i>Acer merriami</i>
<i>Salix coalingensis</i>	<i>Acer negundoides</i>
Juglandaceæ	<i>Acer osmonti</i>
<i>Juglans hesperia</i>	<i>Acer septilobatum</i>
Betulaceæ	Hydrocaryaceæ
<i>Ostrya oregoniana</i>	<i>Trapa prenatans</i>
<i>Betula lacustris</i>	Ericaceæ
<i>Alnus</i> sp.	<i>Arbutus matthesii</i>
	Oleaceæ
	<i>Frazinus coulteri</i>
	Incertæ sedis
	cf. <i>Quercus horniana</i>

From a qualitative viewpoint, there are 4 genera which are dominant in number of species: *Quercus* with 6 species, *Acer* with 5 species, *Pinus* with 3

species, and *Ulmus* with 2 species. The remaining genera are represented by 1 species each. From a quantitative viewpoint, based on leaf counts of over 400 specimens, the order of dominance of the 12 most abundant species is as follows: *Typha lesquereuxi*, *Quercus browni*, *Quercus simulata*, *Acer*

TABLE 1—Local distribution

Species	Hog Creek; Locality 635	North- South Highway; Locality 636	Cove Creek; Locality 637	Alkali Creek; Locality 638
<i>Dryopteris idahoensis</i>				X
<i>Equisetum</i> sp.....	X			X
<i>Pinus knowltoni</i>	X		X	
<i>Pinus tetrafolia</i>	X			
<i>Pinus</i> sp.....		X		
<i>Picea labontense</i>	X			
<i>Pseudotsuga masoni</i>	X		X	
<i>Abies</i> sp.....	X			
<i>Sequoia langsdorffii</i>	X			X
<i>Libocedrus</i> sp.....	X			
<i>Thuja garmani</i>	X			
<i>Juniperus sabinoides</i>	X	X		
<i>Typha lesquereuxi</i>	X	X	X	X
<i>Cyperacites</i> sp.....	X			
<i>Salix coalingensis</i>	X	X	X	X
<i>Juglans hesperia</i>			X	X
<i>Ostrya oregoniana</i>	X			
<i>Betula lacustris</i>	X		X	
<i>Alnus</i> sp.....			X	X
<i>Castanopsis convexa</i>	X	X	X	
<i>Quercus browni</i>	X	X		X
<i>Quercus cognata</i>	X			
<i>Quercus declinata</i>	X			
<i>Quercus duriuscula</i>			X	
<i>Quercus mecani</i>		X	X	
<i>Quercus simulata</i>	X	X	X	X
<i>Ulmus moorei</i>	X	X	X	X
<i>Ulmus speciosa</i>			X	
<i>Platanus dissecta</i>	X		X	X
<i>Cercidiphyllum crenatum</i>	X			
<i>Odostemon simplex</i>	X	X		
<i>Prunus rustii</i>	X			X
<i>Cercocarpus antiquus</i>			X	
<i>Leguminosites</i> sp.....	X			
<i>Ptelea miocenica</i>	X			
<i>Celastrus</i> sp.....	X			
<i>Acer chaneyi</i>	X	X		X
<i>Acer merriami</i>	X			
<i>Acer negundoides</i>	X			
<i>Acer osmonti</i>	X		X	
<i>Acer septilobatum</i>	X			
<i>Trapa prenatans</i>		X		
<i>Arbutus matthesii</i>	X			
<i>Fraxinus coulteri</i>	X	X		X
<i>cf. Quercus horniana</i>			X	
Number of species.....	35	13	17	15
Percentage of total species.....	78	29	38	33

negundoides, *Salix coalingensis*, *Juniperus sabinoides*, *Arbutus matthesii*, *Pseudotsuga masoni*, *Castanopsis convexa*, *Odostemon simplex*, *Platanus dissecta*, and *Fraxinus coulteri*.

LOCAL DISTRIBUTION OF SPECIES

The distribution of the 45 species among the four localities is shown in table 1. Locality 635 is by far the largest of the florules, containing more than twice the number of species in any one of the other localities. *Quercus simulata*, *Salix coalingensis*, *Typha lesquereuxi*, and *Ulmus moorei* are the most wide-ranging species, occurring at 4 localities each; *Acer chaneyi*, *Castanopsis convexa*, *Fraxinus coulteri*, *Platanus dissecta*, and *Quercus browni* occur at 3 localities each; of the remaining species, 14 occur at 2 localities and 22 are restricted to one. Of the 9 most wide-ranging species all but *Ulmus moorei* and *Acer chaneyi* are among the 12 most abundant species at the individual localities as listed on page 81.

PHYSICAL CONDITIONS INDICATED BY THE FLORA

In attempting to determine the physical conditions under which the Weiser flora grew, major considerations will be given to the requirements of those modern species which are closely similar to Weiser species. Less attention will be given to the species which are only remotely comparable or of which several are equally similar to a single Weiser species. The specimens of *Equisetum* sp., *Pinus knowltoni*, *P. tetrafolia*, *Pinus* sp., *Quercus mccanni*, and *Typha lesquereuxi*, for example, do not show sufficient specific details to make possible a close comparison with any single modern species; *Leguminosites* sp., on the other hand, can not even be definitely referred to any one existing genus. Practically all of the remaining species have extremely close relatives among modern species on the basis of similarity of leaves or fruits.

The distribution of the modern equivalents of the Weiser species is summarized in the following compilation, in which the fossil species are shown in parentheses:

A—Europe

1. *Trapa natans* (*T. prenatans*)

B—Eastern Asia

1. *Cercidiphyllum japonicum* (*C. crenatum*)
2. *Quercus myrsinaefolia* (*Q. simulata*)
3. *Ulmus parvifolia* (*U. moorei*)

C—Mexico

1. *Celastrus pringlei* (*Celastrus* sp.)

D—Eastern and Central United States

1. *Acer negundo* (*A. negundoides*)
2. *Acer saccharinum* (*A. chaneyi*)
3. *Juglans nigra* (*J. hesperia*)
4. *Ostrya virginiana* (*O. oregoniana*)
5. *Ptelea trifoliata* (*P. miocenica*)
6. *Ulmus americana* (*U. speciosa*)

E-Western United States

1. *Acer glabrum* (A. osmonti)
2. *Acer negundo* (A. negundoides)
3. *Betula fontinalis* (B. lacustris)
4. *Cercocarpus betuloides* (C. antiquus)
5. *Picea engelmanni* (P. lahontense)
6. *Prunus demissa* (P. rustii)
7. *Pseudotsuga taxifolia* (P. masoni)
8. *Salix lasiolepis* (S. coalingensis)
9. *Thuya plicata* (T. garmani)
10. **Abies amabilis* (Abies sp.)
11. **Acer circinatum* (A. septilobatum)
12. **Acer macrophyllum* (A. merriami)
13. **Alnus rubra* (Alnus sp.)
14. **Arbutus menziesii* (A. matthesii)
15. **Castanopsis sempervirens* (C. convexa)
16. **Fraxinus oregona* (F. coulteri)
17. **Libocedrus decurrens* (Libocedrus sp.)
18. **Odostemon californica* (O. simplex)
19. **Platanus racemosa* (P. dissecta)
20. **Quercus chrysolepis* (Q. browni)
21. **Quercus garryana* (Q. duriuscula)
22. **Quercus morehus* (Q. cognata)
23. **Quercus tomentella* (Q. declinata)
24. **Sequoia sempervirens* (S. langsdorfii)

* Species thus marked are confined to the Pacific states; those unmarked range eastward into the Rocky Mountains.

These lists show that by far the largest percentage, namely 68.5 per cent, of the modern equivalents are found in the western states, and that as many as 42.8 per cent are at present restricted to the Pacific states west of the Rocky Mountains. The single species from Europe and Mexico do not have generic representatives in western North America at present, but are found in the eastern states, where *Celastrus scandens* is native and *Trapa natans* has escaped from cultivation. Of the three Asiatic species only one, *Quercus myrsinaefolia*, is generically represented in the Pacific states. Of the six species of eastern and central United States, *Acer negundo* grows also in the Pacific states, and *Acer saccharinum* and *Juglans nigra* are represented by closely related species. The remaining three genera, *Ostrya*, *Ptelea*, and *Ulmus* are not found at present west of the Rocky Mountains.

It is apparent that the Weiser flora, when considered as a forest association, will find its closest living counterpart in the forests of the Pacific states. An association must be looked for which contains the largest number of modern correlatives of the Weiser species. Little use can be made of those species which do not inhabit the Pacific region at present except for purposes of corroboration.

The distribution of the modern equivalents of the Weiser species according to life zones is shown in table 2. The exotic species from Europe, Asia, and Mexico have been omitted because of lack of information regarding their zonal distribution.

Table 2 clearly shows that the association of living correlatives of the Weiser species is almost wholly an assemblage of Transition zone species.

TABLE 2—Zonal distribution of modern equivalents of the Weiser species

Western species		Lower Sonoran	Upper Sonoran	Transition		Canadian	Hudsonian
Fossil	Living			Arid	Humid		
Abies sp.	Abies amabilis					X	
Acer septilobatum	Acer circinatum				X		
Acer osmonti	Acer glabrum				X	X	
Acer merriami	Acer macrophyllum			X	X		
Acer negundoides	Acer negundo		X	X			
Alnus sp.	Alnus rubra				X	X	
Arbutus matthesii	Arbutus menziesii			X	X		
Betula lacustris	Betula fontinalis			X		X	
Castanopsis convexa	Castanopsis sempervirens			X		X	
Cercocarpus antiquus	Cercocarpus betuloides		X	X	X		
Fraxinus oculteri	Fraxinus oregona			X	X		
Libocedrus sp.	Libocedrus decurrens			X			
Odostemon simplex	Odostemon californica			X			
Picea lahontense	Picea engelmanni					X	
Platanus dissecta	Platanus racemosa		X	X			
Prunus rustii	Prunus demissa			X	X		
Pseudotsuga masoni	Pseudotsuga taxifolia			X	X		
Quercus browni	Quercus chrysolepis		X	X	X		
Quercus duriuscula	Quercus garryana		X	X	X		
Quercus cognata	Quercus morehus			X			
Quercus declinata	Quercus tomentella			X	X		
Salix coalingensis	Salix lasiolepis		X	X	X		
Sequoia langsdorffii	Sequoia sempervirens				X		
Thuja garmani	Thuja plicata				X	X	
Total western occurrences		0	6	17	15	7	0
Percentage of total western species		0	25	71	62.5	29	0

Eastern species		Austro-riparian	Carolinian	Alleghenian	Canadian	Hudsonian
Fossil	Living					
Acer chaneyi	Acer saccharinum		X	X		
Juglans hesperia	Juglans nigra		X	X		
Ostrya oregoniana	Ostrya virginiana		X	X		
Ptelea miocenica	Ptelea trifoliata		X	X		
Ulmus speciosa	Ulmus americana		X	X		
Total eastern occurrences		0	5	5	0	0
Percentage of total eastern species		0	100	100	0	0
Total of both eastern and western occurrences		0	11	25	7	0
Percentage of total eastern and western species		0	38	86	24	0

There are, in fact, only two species, *Abies amabilis* and *Picea engelmanni*, which do not normally thrive in the forests of the Transition zone. Even these are known to occur in scattered outliers of their respective zones within the boundaries of the Transition zone proper, where their leaves, cones, and seeds might easily enter the sedimentary record along with those of typical Transition zone species.

It is significant that of the western Transition species there are seven which are restricted to the Arid Transition zone as against five to the Humid Transition; in total occurrences also the Arid Transition species outnumber the Humid Transition by a ratio of 17 to 15. These figures imply that the Weiser association was composed of species growing under conditions slightly more favorable for the Arid than for the Humid Transition species, yet suitable for both. Such conditions might be fulfilled by valleys extending down from an upper, more humid region into the Arid Transition zone.

Up to this point, the Weiser flora has been considered as a unit. In the following discussion, the florules from each of the four localities will be treated as individual forest associations. This will tend to present a more accurate picture of the forests which grew at various intervals of time, since the stratigraphic separation of the plant localities indicates that the four florules may not have been strictly contemporaneous.

LOCALITY 635

This florule is by far the largest of the four. It is composed of 35 species, listed on page 81, of which 21 have their closest living relatives in the Pacific states, 3 in Eastern and Central United States, 3 in Eastern Asia, and 1 in Mexico. The remaining 7 species can not be compared with any single living species. In the attempt to find a living forest which is most nearly equivalent to the forest association from this locality, it is obvious from these figures that no living forest exists which contains all the living equivalents growing together. Seven fossil species have left no closely related species in the Pacific coast flora since late Tertiary time, and five of these have not even survived there generically. From a study of the remaining 21 living equivalents of the Pacific states, it may be possible, however, to locate a region in which a large majority of species are still associated in a single forest community.

The distribution of these 21 species according to life-zones, as derived from the data of table 2 may be summarized as follows:

	Species
Upper Sonoran zone occurrences.....	4
Transition zone occurrences.....	19
Arid Transition.....	15
Humid Transition.....	12
Canadian zone occurrences.....	6

This tabulation indicates that whereas many species tend to range from one zone or subzone into another, 19 of the total 21 are ecologically adapted to Transition zone conditions. More important, perhaps, is the observation that of the 15 species which thrive in the Arid Transition zone, 7 species do not extend into the Humid Transition, and that of the 12 species which thrive in the Humid Transition, only 4 species do not extend into the Arid Transition. These figures imply that in each category the Arid Transition species tend to outnumber those of the Humid Transition by a slight margin. The association to be looked for among the Pacific coast forests seems then to be one which is located within the boundaries of the Arid Transition zone, yet close to the border of the Humid Transition.

The geographic distribution of living equivalents in the Pacific states is shown in Section A of table 3, from which it is possible to confine attention to smaller areas within which the largest number of species are found together. The summary totals in this section indicate that although as many as 11 species range northward into British Columbia, the proportion increases toward the south into California, where 20 of the 21 species are found. It is significant, moreover, that of these 20 species there are 5 which are confined to the California region. Such species are obviously of greater importance as indicators or index species than the species of wide geographic range, and tend to accentuate the California aspect of the association from Locality 635.

Having thus concentrated attention on the California region, it is necessary to continue to eliminate the least favorable areas and limit the search to such areas as contain the largest proportion of associated species. To such an end Section B of table 3 has been arranged. The Cascade region of southern Oregon has been included because of its proximity and close relationships to the forests of California. It is at once obvious that the northern Coast Ranges, containing 17 of the 21 species, offer the most likely area in which to look for an association most nearly equivalent to the fossil association from Locality 635.

The humid outer Coast Ranges of northern California are occupied by the redwood forest of the coast forest climax. This forest is dominated by *Sequoia sempervirens* and its mesic associates of the Humid Transition zone. The most important species and their related fossil species from Locality 635 are shown in the following list. The relative order of dominance of the fossil species in the leaf count of 232 specimens is indicated in percentages. Specific representations of less than one per cent of the total number of specimens are omitted. The species marked by an asterisk (*) are those which, though closely related to the accompanying modern species, are not necessarily the most closely related. *Quercus simulata*, for example, seems to be most closely similar to the Asiatic species *Q. myrsinæfolia*, yet appears to be represented ecologically in the west coast forests by *Lithocarpus densiflora*.

TABLE 3—Geographic distribution of modern western equivalents of the species from Locality 685

Fossil species	Living species	Sec. A. Pacific States (north to south)				Sec. B. Southern Oregon and California				
		British Columbia	Washington	Oregon	California	Cascades of S. Oregon	Mt. Shasta Region of N. California	Sierras of California	Northern Coast Ranges of California	Southern Coast Ranges of California
<i>Abies</i> sp.	<i>Abies amabilis</i>	xxxxxx	xxxxxx	xx		X	X		X	
<i>Acer septilobatum</i>	<i>Acer circinatum</i>	xxxxxx	xxxxxx	xxxxxx	xx	X	X		X	
<i>Acer osmondii</i>	<i>Acer glabrum</i>	xxxxxx	xxxxxx	xxxxxx	xxx	X	X		X	X
<i>Acer merriami</i>	<i>Acer macrophyllum</i>	xxxxxx	xxxxxx	xxxxxx	xxxx	X	X		X	X
<i>Acer negundooides</i>	<i>Acer negundo</i>	xxxxxx	xxxxxx	xxxxxx	xxxxxx			X		
<i>Arbutus matthesii</i>	<i>Arbutus menziesii</i>	xxx	xxxxxx	xxxxxx	xxxxxx	X	X		X	
<i>Betula lacustris</i>	<i>Betula fontinalis</i>	xxxxxx	xxxxxx	xxxxxx	xxxxxx	X	X		X	X
<i>Castanopsis convexa</i>	<i>Castanopsis sempervirens</i>	xxxxxx	xxxxxx	xxxxxx	xxxxxx	X	X		X	X
<i>Fraxinus coulteri</i>	<i>Fraxinus oregana</i>	xxx	xxxxxx	xxxxxx	xxxxxx	X	X		X	X
<i>Libocedrus</i> sp.	<i>Libocedrus decurrens</i>		xxxxxx	xxxxxx	xxxxxx	X	X		X	X
<i>Odoestemon simplex</i>	<i>Odoestemon californica</i>									
<i>Picea lahontense</i>	<i>Picea engelmannii</i>									
<i>Platanus dissecta</i>	<i>Platanus racemosa</i>	xxxxxx	xxxxxx	xxxxxx	xxxxxx	X	X		X	X
<i>Prunus rustii</i>	<i>Prunus demissa</i>	xxxxxx	xxxxxx	xxxxxx	xxxxxx		X		X	X
<i>Pseudotsuga masoni</i>	<i>Pseudotsuga taxifolia</i>	xxxxxx	xxxxxx	xxxxxx	xxxxxx	X	X		X	X
<i>Quercus browni</i>	<i>Quercus chrysolepis</i>			xxx	xxxxxx			X	X	X
<i>Quercus cognata</i>	<i>Quercus morehus</i>				xxxx					
<i>Quercus declinata</i>	<i>Quercus tomentella</i>				xxxxxx					
<i>Salix coalingensis</i>	<i>Salix lasiolepis</i>		xxxxxx	xxxxxx	xxxxxx		X		X	X
<i>Sequoia langsdorffii</i>	<i>Sequoia sempervirens</i>	xxxxxx	xxxxxx	xxxxxx	xxxxxx				X	
<i>Thuja garmani</i>	<i>Thuja plicata</i>	xxxxxx	xxxxxx	xxxxxx	xx	X			X	
Total occurrences in each area		11	12	16	20	12	12	15	17	14
Total species restricted to each area		0	0	0	5	1	0	0	0	0

OUTER COAST RANGES

Redwood Forest	Related Fossil Species	p. ct.
<i>Picea sitchensis</i>	* <i>Picea lahontense</i>	-----
<i>Tsuga heterophylla</i>	none	-----
<i>Pseudotsuga taxifolia</i>	<i>Pseudotsuga masoni</i>	2.6
<i>Abies grandis</i>	* <i>Abies</i> sp.	-----
<i>Sequoia sempervirens</i>	<i>Sequoia langsdorfii</i>	1.7
<i>Thuya plicata</i>	<i>Thuya garmani</i>	-----
<i>Torreya californica</i>	none	-----
<i>Myrica californica</i>	none	-----
<i>Corylus rostrata</i> var. <i>californica</i>	none	-----
<i>Alnus rubra</i>	none	-----
<i>Castanopsis chrysophylla</i> var. <i>minor</i>	* <i>Castanopsis convexa</i>	6.5
<i>Lithocarpus densiflora</i>	* <i>Quercus simulata</i>	12.5
<i>Odostemon nervosa</i>	* <i>Odostemon simplex</i>	1.7
<i>Umbellularia californica</i>	none	-----
<i>Acer macrophyllum</i>	<i>Acer merriami</i>	-----
<i>Acer circinatum</i>	<i>Acer septilobatum</i>	-----
<i>Rhamnus purshiana</i>	none	-----
<i>Cornus nuttallii</i>	none	-----
<i>Rhododendron occidentale</i>	none	-----
<i>Quercus agrifolia</i>	none	-----
Totals 20 species	10 species	25.0+

There is apparently some degree of relationship between the association from Locality 635 and the modern redwood forest. Ten of the total 21 fossil species (disregarding those which have no existing relatives on the Pacific coast and those whose specific correlation is vague), which constitute about 25 per cent of the total number of specimens, are represented by modern related species. It is significant to point out, however, that only 5 species have their most closely related modern species in the redwood forest, and that two of the related modern species, namely, *Pseudotsuga taxifolia* and *Lithocarpus densiflora*, are more important on the borders of the redwood forest and in the inner coast range forests discussed below than in the outer Coast Ranges. Also, *Castanopsis convexa* is much more closely related to the modern *C. sempervirens* of the inner Coast Ranges than to the redwood species, *C. chrysophylla* var. *minor*. Notably absent, moreover, from the fossil association are the more mesic equivalents of the redwood forest species, such as *Tsuga heterophylla*, *Torreya californica*, *Alnus rubra*, *Rhamnus purshiana*, *Cornus nuttallii*, and *Rhododendron occidentale*. Equally significant is the fact that the more mesic of the fossil species, such as *Sequoia langsdorfii*, *Picea lahontense*, *Abies* sp., *Acer merriami*, and *A. septilobatum* are extremely rare in the collections.

In the inner Coast Ranges of northern California the mesic redwood forest grades inland into more open border phases which soon give way under

Arid Transition conditions to the wide-spread broad-sclerophyll forest.¹ In the lower altitudes, the most important subdivision of this forest is the *Lithocarpus*²-*Quercus*-*Arbutus* community, which is often associated with chaparral, grassland, and stream-border communities. In the following list, arranged with related fossil species and percentages as above, the species are divided into three categories: (1) Those species which are commonly associated in the *Lithocarpus*-*Quercus*-*Arbutus* community near the inner border of the redwood forest,³ (2) those species which are characteristic of the associated pine forest community,⁴ and (3) those species which often form stream-border or riparian communities within the *Lithocarpus*-*Quercus*-*Arbutus* community.⁵

INNER COAST RANGES

(1) <i>Lithocarpus</i> - <i>Quercus</i> - <i>Arbutus</i> Community	Related Fossil Species	p. ct.
<i>Pseudotsuga taxifolia</i>	<i>Pseudotsuga masoni</i>	2.6
<i>Lithocarpus densiflora</i>	* <i>Quercus simulata</i>	12.5
<i>Quercus chrysolepis</i>	<i>Quercus browni</i>	21.6
<i>Arbutus menziesii</i>	<i>Arbutus matthesii</i>	4.3
<i>Castanopsis chrysophylla</i>	none	----
<i>Quercus kelloggii</i>	* <i>Quercus cognata</i>	1.3
<i>Umbellularia californica</i>	none	----
<i>Acer macrophyllum</i>	<i>Acer merriami</i>	----
<i>Æsculus californica</i>	none	----
<i>Cornus nuttallii</i>	none	----
<i>Abies concolor</i>	* <i>Abies</i> sp.	----
<i>Pinus lambertiana</i>	* <i>Pinus tetrafolia</i>	----
<i>Odostemon</i> sp.	* <i>Odostemon simplex</i>	1.7
<i>Quercus garryana</i>	none	----
<i>Pinus ponderosa</i>	<i>Pinus</i> sp.	1.3
<i>Sequoia sempervirens</i> (rare)	<i>Sequoia langsdorfii</i>	1.7
<i>Libocedrus decurrens</i>	<i>Libocedrus</i> sp.	----
(2) Associated Pine Forest Species		
<i>Acer glabrum</i>	<i>Acer osmonti</i>	2.6
<i>Castanopsis sempervirens</i>	<i>Castanopsis convexa</i>	6.5
<i>Prunus demissa</i>	<i>Prunus rustii</i>	1.3
(3) Associated Riparian Species		
<i>Salix lasiolepis</i>	<i>Salix coalingensis</i>	4.3
<i>Fraxinus oregona</i>	<i>Fraxinus coulteri</i>	2.2
<i>Populus trichocarpa</i>	none	----
<i>Betula fontinalis</i>	<i>Betula lacustris</i>	----
<i>Cratægus rivularis</i>	none	----
<i>Equisetum</i> spp.	* <i>Equisetum</i> sp.	1.7
<i>Typha latifolia</i>	* <i>Typha lesquereuxi</i>	----
Totals	27 species	20 species
		65.6+

¹ Cooper, Carnegie Inst. Wash. Pub. No. 319, 21, 1922.

² *Pasania* of Cooper.

³ Cooper, *op. cit.*, page 22.

⁴ Cooper, *op. cit.*, page 28.

⁵ Chaney, Carnegie Inst. Wash. Pub. No. 349, 39, 1925.

Here apparently is a forest community which shows a striking similarity to the fossil association from Locality 635. Out of a total of 26 fossil species which have related living species in the Pacific states, 20 are here represented, making up 77 per cent of the total species which might be expected to occur and over 65 per cent of the total specimens collected. The remaining 6 fossil species, which are not characteristically associated with the *Lithocarpus-Quercus-Arbutus* community of the northern Coast Ranges, are listed below with the percentage of each species of the total number collected:

Closely Related Modern Species	Fossil Species	p. ct.
<i>Acer negundo</i>	<i>Acer negundoides</i>	10.8
<i>Quercus tomentella</i>	<i>Quercus declinata</i>	1.7
<i>Acer circinatum</i>	<i>Acer septilobatum</i>	-----
<i>Picea engelmanni</i>	<i>Picea lahontense</i>	-----
<i>Thuja plicata</i>	<i>Thuja garmani</i>	-----
<i>Platanus racemosa</i>	<i>Platanus dissecta</i>	-----
		<hr/> 12.5

On the basis of modern California associations, it is not difficult to suggest an explanation for the presence of all of these species in an association of the *Lithocarpus-Quercus-Arbutus* type. *Acer circinatum* and *Thuja plicata* are both common associates of the redwood forest and are known to extend locally into its border phases where they could easily contribute enough occasional seeds or twigs to make up the less than one per cent by which their fossil equivalents are represented in the collections. *Platanus racemosa* is at present not found in the northern Coast Ranges, but is abundant in the *Lithocarpus-Quercus-Arbutus* association of the southern Coast Ranges near the southern limits of the redwood forest.¹ *Acer negundo*, whose fossil equivalent ranks third in the collections in order of dominance with a percentage of 10.8, is a valuable indicator since it is at present restricted to the less mesic portions of the inner Coast Ranges of central and southern California. That it is not out of place in the more open portions of the *Lithocarpus-Quercus-Arbutus* community is indicated by its association in the Clear Lake region of the north-central Coast Ranges with such characteristic species as *Pseudotsuga taxifolia*, *Quercus kelloggii*, *Arbutus menziesii*, and *Fraxinus oregona*.² *Picea engelmanni* is chiefly confined to the Canadian zone, but does not at present extend into northern California. In the adjacent Cascades of Oregon and into Washington, however, the Canadian zone merges downward into the Transition zone,³ particularly on the more arid eastern slopes, and *Picea engelmanni* comes rather closely in contact with typical species of the *Lithocarpus-Quercus-Arbutus* com-

¹ Dorf, Carnegie Inst. Wash. Pub. No. 412, 41, 1930.

² Jepson, *Erythea*, vol. 1, 10, 1893.

³ Piper, *Contrib. Nat. Herbarium*, vol. 11, 58, 1906.

munity.¹ The remaining species, *Quercus tomentella*, is at present confined to the islands off the southern California coast, where it is associated with live oaks, chaparral, and riparian species which suggest a close ecological similarity to the *Lithocarpus-Quercus-Arbutus* community of the mainland.

In the list on page 89 there are several modern species of the *Lithocarpus-Quercus-Arbutus* community which are not represented by equivalent fossil species from this locality. Their absence seems rather significant in postulating climatic requirements. *Castanopsis chrysophylla*, *Umbellularia californica*, and *Cornus nuttallii*, for example, are all much more characteristic of the Humid Transition forests of the outer Coast Ranges than of the Arid Transition forests of the inner Coast Ranges. Their absence from representation among the fossil species would seem to accentuate the somewhat xeric character of the association.

From the foregoing discussion, it may be stated in summary that of the 35 fossil species from Locality 635, 26 species representing 74.3 per cent of the total species and 78.1 per cent of the total number of specimens collected, closely resemble or are ecologically equivalent to living species which thrive in the *Lithocarpus-Quercus-Arbutus* community of the inner Coast Ranges of northern California or live in close contact with this community in the same region or elsewhere in California or Oregon. It is essential, therefore, to specify the climatic and physical requirements of this community in attempting to determine the requirements of its fossil counterpart.

The *Lithocarpus-Quercus-Arbutus* community is the northern Coast Ranges representative of the broad-sclerophyll vegetation of California, which has been studied by Cooper.² In general the climatic conditions for this type of vegetation are mild temperatures with moderate extremes, winter rains and prolonged summer drought. The mean annual temperature averages about 58°F., with a mean minimum of 37°F., and a mean maximum of 84°F. The mean annual precipitation is about 22 inches, of which about 12 per cent falls during the summer months from May to October. Cooper points out, however, that where the broad-sclerophylls become transitional to the redwood forest of the northern Coast Ranges, the mean annual precipitation increases to about 38 inches, of which about the same percentage of 12 per cent falls during the summer. Since the *Lithocarpus-Quercus-Arbutus* community which shows closest comparison with the fossil association is clearly a mixed broad-sclerophyll conifer community, the rainfall requirements must lie somewhere between 22 inches and 38 inches. As the broad-sclerophylls dominate the fossil association in both number of species and percentage of total specimens, the rainfall probably averaged between 25 and 30 inches per year.

A general idea of the topographic and altitudinal requirements of the fossil association may be derived, also, from a study of the distribution of

¹ Leiberg, U. S. Geol. Surv., Twenty-first Ann. Rept., pt. 5, 235, 1900.

² Cooper, Carnegie Inst. Wash. Pub. No. 319, 1922.

the modern *Lithocarpus-Quercus-Arbutus* community. This community is characteristic of the lower altitudes of the north Coast Ranges. The greatest number of species which show close relationship to the fossil species from Locality 635 are found together at altitudes of 1500 to 3000 feet. This is essentially the altitude and amount of relief which seem to have obtained in the Weiser area at the time of the deposition of the plant-bearing sediments.

There still remain 9 species in the collection from Locality 635 which have not been discussed because of their indefinite specific status or because they are closely related to species not now existing in the Pacific states. These are listed below with their nearest living relatives and their percentage representation in the collections:

Related Modern Species	Fossil Species	p. ct.
<i>Juniperus californica</i> }	<i>Juniperus sabinoides</i>	6.5
<i>Juniperus occidentalis</i> }		
<i>Acer saccharinum</i>	<i>Acer chaneyi</i>	1.7
<i>Ptelea trifoliata</i>	<i>Ptelea miocenica</i>	1.7
<i>Ulmus parvifolia</i>	<i>Ulmus moorei</i>	1.3
<i>Cercidiphyllum japonicum</i>	<i>Cercidiphyllum</i>	
	<i>crenatum</i>	----
<i>Cercis occidentalis</i>	<i>Leguminosites</i> sp.	----
<i>Celastrus pringlei</i>	<i>Celastrus</i> sp.	----
<i>Ostrya virginiana</i>	<i>Ostrya oregoniana</i>	----
<i>Cyperus</i> spp. }	<i>Cyperacites</i> sp.	----
<i>Carex</i> spp. }		
	Total	11.2

The two modern correlatives of *Juniperus sabinoides*, which ranks fourth in order of dominance in the collections, are living in the Pacific region under conditions quite different from each other. *Juniperus californica* is extremely rare in the northern Coast Ranges. It is characteristic of dry hill-sides of southern California and the southern Sierra Nevada, in an association which is normally more xeric than the *Lithocarpus-Quercus-Arbutus* community. The closely similar *J. occidentalis*, however, is wide-spread in the Transition and Canadian zones of western Oregon, the Cascades and the Sierra Nevada,¹ and is associated with as many as ten characteristic species of the *Lithocarpus-Quercus-Arbutus* community in the Mount Shasta region of north central California.² *Cercis occidentalis* is common along foothill streams of northern California, and is also found in association with characteristic species of the *Lithocarpus-Quercus-Arbutus* community. *Acer saccharinum*, *Ptelea trifoliata*, and *Ostrya virginiana* are wide-spread in the humid eastern United States, but extend westward to the semiarid Great Plains, where they are common along streams in a region

¹ Harshberger, *Phytogeographic Survey of North America*, 265-268, 1911.

² Merriam, C. Hart, *N.A. Fauna*, No. 16, 58, 1899.

with an annual rainfall of 20 to 30 inches. *Ulmus parvifolia* is characteristic of the semixerix habitats of eastern Asia, thriving under an annual rainfall of about 25 inches. *Cercidiphyllum japonicum* grows best under conditions of adequate precipitation throughout the year, but grows sparingly in regions with a rainfall of 20 to 30 inches and a dry season during the winter months.¹ Additional indication that the fossil equivalent, *Cercidiphyllum crenatum*, is not unsuited to somewhat xeric conditions is shown by its presence in a Lower Pliocene flora from Oklahoma² in which the vegetation is distinctly of semiarid type. Both there and in Idaho, however, this species is much less abundantly represented than in the older and more mesic Miocene floras of the John Day Basin. *Celastrus pringlei* grows in the Mexican highlands under rainfall of 30 to 40 inches or less and is associated with species of *Pinus*, *Quercus* (both live oaks and black oaks), *Alnus*, *Salix*, *Arbutus*, and *Acer*³ in a community which strikingly resembles the *Lithocarpus-Quercus-Arbutus* community of California. The remaining species of *Cyperus* or *Carex*, representing the fossil species *Cyperacites* sp., are of no particular climatic significance, as species of these genera are ubiquitous under all types of conditions. In California alone there are 126 species of *Carex* and 12 species of *Cyperus*,⁴ many of which are common in the *Lithocarpus-Quercus-Arbutus* community.

It is apparent, therefore, that although a number of species have been eliminated from the flora of western North America since Late Tertiary time, their present climatic requirements in other regions are in no way inconsistent with the postulated conditions for the flora from Locality 635.

LOCALITY 636

The flora from this locality comprises 13 species, which are listed in table 1. All but 2 of the species are present also at Locality 635. Nine of the species are closely similar to living species of the *Lithocarpus-Quercus-Arbutus* community and related communities, as shown below:

(1) Lithocarpus-Quercus-Arbutus Community	Related Fossil Species
Lithocarpus densiflora	*Quercus simulata
Quercus chrysolepis	Quercus browni
Pinus ponderosa	Pinus sp.
Odostemon sp.	Odostemon simplex
Juniperus occidentalis	*Juniperus sabinoides
(2) Associated Pine Forest Species	
Castanopsis sempervirens	Castanopsis convexa
(3) Associated Riparian Species	
Salix lasiolepis	Salix coalingsensis
Fraxinus oregona	Fraxinus coulteri
Typha latifolia	*Typha lesquereuxii

¹ LaMotte, Carnegie Inst. Wash. Pub. No. 455, 1936.

² Chaney and Elias, Carnegie Inst. Wash. Pub. No. 476, 1936.

³ Chaney, oral communication, December 1935.

⁴ Jepson, *Manual of the Flowering Plants of California*, 145, 1925.

This association is clearly of the same general type as has already been discussed in connection with the flora from Locality 635. The absence of the more mesic species of the *Lithocarpus-Quercus-Arbutus* community, such as *Pseudotsuga masoni*, *Arbutus menziesii*, *Quercus cognata*, *Acer merriami*, and *Sequoia langsdorfi*, which were present in the flora from Locality 635, suggest that conditions were somewhat drier, with a probable annual rainfall of slightly less than 25 inches.

Of the species from this locality which do not have living equivalents in the flora of western North America, *Ulmus moorei* and *Acer chaneyi* have already been shown (see p. 92) to be tolerant to an annual rainfall of 20 to 30 inches. *Quercus mccanni* resembles the chestnut-oaks of eastern North America which extend into the southern Great Plains where the annual rainfall is likewise between 20 and 30 inches. The remaining species, *Trapa prenans*, is of little climatic significance since its living equivalent, *T. natans*, is a hydric species growing under water and is tolerant of a wide range of rainfall conditions.

LOCALITY 637

As shown in table 1, this flora is composed of 17 species of which 7 species are not reported from Locality 635. Eleven of the species have living relatives in the *Lithocarpus-Quercus-Arbutus* community and related communities as follows:

(1) Lithocarpus-Quercus-Arbutus Community	Related Fossil Species
Pseudotsuga taxifolia	Pseudotsuga masoni
Lithocarpus densiflora	*Quercus simulata
Quercus garryana	Quercus duriuscula
Pinus ponderosa	Pinus knowltoni
(2) Associated Pine Forest Species	
Acer glabrum	Acer osmonti
Castanopsis sempervirens	Castanopsis convexa
Cercocarpus betuloides	Cercocarpus antiquus
(3) Associated Riparian Species	
Salix lasiolepis	Salix coalingensis
Betula fontinalis	Betula lacustris
Alnus rubra	Alnus sp.
Typha latifolia	*Typha lesquereuxi

In this association, there is a larger proportion of riparian and pine forest species than was present in the floras from Localities 635 and 636, suggesting somewhat more xeric conditions. Of the six exotic species which do not have living relatives in the communities above, *Platanus dissecta*, *Ulmus moorei*, and *Quercus mccanni* have already been discussed in connection with the floras from Localities 635 and 636. *Juglans hesperia* is related to the living *J. nigra*, which is typical of eastern United States, but extends westward into the Great Plains under rainfall conditions of 20 to 30 inches

annually. *Ulmus speciosa* finds its closest living relative in *U. americana*, which is abundant in the mesic forests of eastern North America but is also tolerant of the semiarid conditions of the Great Plains as far west as the Black Hills and western Nebraska, with an annual rainfall of 10 to 20 inches. The remaining species, cf. *Quercus horniana*, has no climatic significance because of its uncertain relationships to modern species.

The entire association from this locality, therefore, is suggestive of a somewhat more xeric assemblage than is present at Localities 635 and 636 and indicates a climate with somewhat lower rainfall, probably approaching 20 inches annually.

LOCALITY 638

As shown in table 1, there are 15 species in the flora from this locality. All but three of the species are in common with the larger flora of Locality 635. Nine of the species are closely related to the *Lithocarpus-Quercus-Arbutus* community and associated communities:

(1) Lithocarpus-Quercus-Arbutus Community	Related Fossil Species
Lithocarpus densiflora	*Quercus simulata
Quercus chrysolepis	Quercus browni
Sequoia sempervirens	Sequoia langsdorffii
(2) Associated Pine Forest Species	
Prunus demissa	Prunus rustii
(3) Associated Riparian Species	
Salix lasiolepis	Salix coalingsensis
Fraxinus oregona	Fraxinus coulteri
Alnus rubra	Alnus sp.
Equisetum spp.	Equisetum sp.
Typha latifolia	*Typha lesquereuxii

Here again, the higher proportion of riparian and pine forest species suggests a somewhat xeric assemblage. The presence of *Sequoia langsdorffii* might at first seem to indicate humid conditions. In the living forests, however, the modern *Sequoia sempervirens* is not intolerant to rainfall of 20 to 30 inches, as found in the Santa Lucia Mountains of the southern Coast Ranges of California. In such situations, the riparian and pine forest species are relatively more abundant than in the mesic forests of the more humid outer Coast Ranges of northern California.¹ The resemblance of the flora from this locality to conditions in the southern Coast Ranges is accentuated by the presence of *Platanus dissecta*, whose living equivalent, *Platanus racemosa*, is characteristic of the drier southern Coast Ranges and does not extend into the mesic forests of northern California. Of the remaining species from Locality 638, *Ulmus moorei*, *Cercidiphyllum crenatum*, *Juglans hesperia*, and *Acer chaneyi* have already been discussed under the floras from other localities, as characteristic or tolerant of somewhat xeric conditions of growth. The remaining species, *Dryopteris idahoensis*, is of little

¹ Shreve, Ecology, vol. 8, No. 1, 27, 1927.

climatic significance because of its uncertain relationship to existing species which are wide-spread under many different conditions in western North America.

The complete association from this locality suggests a more xeric assemblage than the floras from Localities 635 and 636. It appears to be ecologically of the same type as the flora from Locality 637 and is likewise indicative of an annual rainfall of less than 25 inches and possibly as low as 20 inches.

SUMMARY OF PHYSICAL CONDITIONS

On the basis of comparison with closely related living species, the associations from the four Weiser localities have been shown to bear a rather close resemblance to the modern *Lithocarpus-Quercus-Arbutus* community and its closely contiguous pine forest and riparian communities. These related communities are growing together in regions of rather mild temperature, dry summers, and medium rainfall. Such conditions are in striking contrast to those now prevailing in the region from which the Weiser flora was collected, and differ in many important respects from the earlier Miocene conditions in the same general region, as inferred from the Bridge Creek, Mascall and Payette floras. Unfortunately there are no Pliocene floras known from the immediate vicinity with which to make climatic comparisons. The Alturas flora¹ from northeastern California, however, may be regarded as representative of the Pliocene of the same general region since it lies east of the Pacific ranges at a distance of less than 250 miles southwest of the Weiser area.

In the following table the contrasting climatic data are based on present conditions in regions whose forests show the closest relationship to the fossil floras concerned. The Bridge Creek flora, for example, has its nearest living equivalent in the redwood forest of coastal California,² the Mascall and Payette floras in the inner and southern borders of the redwood forest,³ and the Alturas flora in the dry inner valleys of northeastern California.⁴ The various types of data given in the table have been selected because of their practical value to the study of plant ecology and distribution, and have been derived from the valuable charts, tables, and graphs presented by Livingston and Shreve.⁵ All figures are given in terms of averages, which have in some instances, because of the high increments used, led to more generalized information than might have been desired.

It is apparent from the table below that the general premise of a gradual cooling accompanied by a steady decrease in annual precipitation in the late Tertiary is amply corroborated by the present study. It is significant

¹ Dorf, Carnegie Inst. Wash. Pub. No. 412, 23, 1930.

² Chaney, Carnegie Inst. Wash. Pub. No. 349, 5, 12, 22, 1925.

³ Chaney, *loc. cit.*, 39, 1925.

⁴ Dorf, Carnegie Inst. Wash. Pub. No. 412, 51, 1930.

⁵ Livingston and Shreve, Carnegie Inst. Wash. Pub. No. 319, 160, 200, 243, 254, 280, 1922.

to note that despite the apparent increase in the normal mean temperature of the hottest six weeks and the increase in number of days with daily normal mean above 68°F, the normal mean annual temperature has decreased from the Miocene to the Pliocene and Recent. This has been due to the accompanying gradual but steady decrease in minimum temperatures, as expressed in the decrease of temperature of the coldest two weeks, the increase in number of days below 32° F, the great decrease in the lowest

Climatic Data	Lower Miocene Bridge Creek Flora	Middle Miocene to Upper Miocene Mascall and Payette Floras	Upper Miocene to Lower Pliocene Weiser Flora	Middle Pliocene to Upper Pliocene Alturas Flora	Recent Present Flora
Normal mean annual temperature	57.5°F	57.5°F	57.5°F	50°F	50°F
Normal mean temperature of hottest 6 weeks	64.4°F	64.4°F	64.4°F	68°F	71.6°F
Number of days with normal daily mean above 68°F.....	0	15	15	45	45
Normal mean temperature of coldest 2 weeks	50.5°F	47.5°F	47.5°F	37.5°F	27.5°F
Number of days with normal daily mean below 32°F.....	0	0	0	15	75
Lowest temperatures observed	20°F	20°F	15°F	minus 10°F	minus 25°F
Length in days of average frostless season.	254	230	215	180	141
Normal mean annual precipitation	50 in.	35 in.	25 in.	17.5 in.	12 in.
Average rainfall during frostless season.	16.5 in.	12.5 in.	11 in.	6.5 in.	5 in.
Percentage of period of frostless season with daily precipitation of 0.1 inch or less	75 p. ct.	80 p. ct.	85 p. ct.	100 p. ct.	100 p. ct.
Mean relative air humidity for period of frostless season....	80 p. ct.	77.5 p. ct.	72.5 p. ct.	45 p. ct.	45 p. ct.
Moisture—evaporation province	Humid	Semihumid	Semihumid	Semiarid	Semiarid

temperatures observed, and the decrease in the length of the frostless seasons. Expressed in general terms, temperature conditions have changed from moderate with low range of variation and few extremes of excessively high or low temperatures in the Lower Miocene to successively less and less moderate temperatures with higher range of variation and greater extremes in the succeeding epochs up to the present. The figures for rainfall and

relative humidity show a steady, gradual decrease both in actual amount and available amount during the frostless season, as adequately expressed in the change from the humid conditions of the Lower Miocene to semihumid in the Middle and Upper Miocene and Lower Pliocene and to semiarid in the remainder of the Pliocene and the Recent.

As has been pointed out by various authors,¹ it is difficult to determine how much of the late Tertiary cooling and drying is due to secular changes in climate and how much is directly a result of changes in topography. The changes in this region have no doubt been largely influenced by the rise of the Pacific Ranges along the west coast, which thus became effective rainfall barriers and eliminated the moderating effects of the Pacific Ocean from regions in the interior.

AGE OF THE FLORA

In determining the age of the flora, three lines of evidence will be presented: first, the distribution in time and space of the Weiser species; second, the comparison of dominant species with dominants of other floras; and third, the comparison of ecological and climatic conditions with those of other floras.

Of the total 45 recognized Weiser species 35, or 78 per cent, have been previously reported from other Tertiary floras of the west. Their distribution is shown in table 4 which indicates that 14 to 15 species occur in the Payette, Upper Cedarville, and Trout Creek floras, 13 to 15 in the Latah, and 13 to 14 in the Mascall. There is also an apparent relationship with the Austin-Tipton flora and the Payette-Latah of Idaho. All of these floras have been recently studied or reviewed and have been assigned to the Upper Miocene; in the majority of cases this age assignment on the basis of floral evidence has been substantiated by evidence derived from the stratigraphy and from associated vertebrate faunas. The Payette flora has recently been referred to the Upper Miocene by both Berry² and LaMotte.³ The Sucker Creek flora, collected from the Payette formation, has also been considered of Upper Miocene age.⁴ The Sucker Creek vertebrate fauna is assigned to the transition between Middle and Upper Miocene and is correlated with the Mascall fauna.⁵ The evidence for the Upper Miocene age of the Mascall, on the basis of its flora, stratigraphy, and associated vertebrates and invertebrates, has recently been reviewed by LaMotte, who also presents stratigraphic, floral, and faunal evidence for the Upper Miocene

¹ Chaney and Elias, Carnegie Inst. Wash. Pub. No. 476, 1936; LaMotte, Carnegie Inst. Wash. Pub. No. 455, 1936; Dorf, Carnegie Inst. Wash. Pub. No. 412, 62, 1930.

² Berry, U. S. Geol. Surv. Prof. Pap. 154-H, 235, 1929.

³ LaMotte, Carnegie Inst. Wash. Pub. No. 455, table 12, 1936.

⁴ Brooks, Annals Carnegie Mus., vol. 24, 286, 1935.

⁵ Stirton, Oral Communication, Dec. 1935.

age of the Upper Cedarville formation.¹ The Latah,² Trout Creek,³ and the Austin-Tipton⁴ floras are compared with the Mascall and likewise referred to the Upper Miocene.

From the foregoing discussion, it is apparent that on the basis of those species which have previously been reported from other fossil floras, the Weiser flora is related to several floras of rather definite Upper Miocene age. Such a correlation, however, disregards those Weiser species which have not previously been reported in the fossil state. For this reason, the following list has been arranged, showing the distribution of those species which appear to be most nearly similar to the remaining Weiser species. Two species, *Equisetum* sp. and *Pinus* sp., have been omitted because of the inadequate material by which they are represented.

Fossil Species	Nearest Related Species	Age
<i>Abies</i> sp.	<i>Abies amabilis</i>	Recent
<i>Alnus</i> sp.	<i>Alnus rubra</i>	Recent
<i>Celastrus</i> sp.	<i>Celastrus pringlei</i>	Recent
<i>Cyperacites</i> sp.	<i>Cyperacites</i> sp.	Lower Pliocene— High Plains
<i>Fraxinus coulteri</i>	<i>Fraxinus oregona</i>	Recent
<i>Leguminosites</i> sp.	Unnamed pod	Lower Miocene— Bridge Creek
<i>Libocedrus</i> sp.	<i>Libocedrus decurrens</i>	Recent
<i>Trapa prenatans</i>	<i>Trapa natans</i>	Recent

The large number of species in this list whose nearest related species are confined to Recent time is no doubt greatly accentuated by the fact that Pliocene floras, in which many or all of these species might be expected to occur, are virtually unknown from the areas in which the numerous Upper Miocene floras occur. The inclusion of these 8 species with the 35 in table 4 gives the following summary of distributional data according to epochs or divisions of epochs:

	Total Species	Species Restricted to Each Division
Lower Miocene	14	1
Upper Miocene	32	12
Pliocene	7	4
Recent	6	6

Here again the closest relationship of the Weiser flora appears to be with the Upper Miocene. Of the 14 Weiser species occurring in the Lower Miocene only one species is restricted to the Lower Miocene, leaving 13

¹ LaMotte, Carnegie Inst. Wash. Pub. No. 455, 1936.

² Berry, *op. cit.*

³ MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 43, 1933.

⁴ Oliver, Carnegie Inst. Wash. Pub. No. 455, 12, 1934.

TABLE 4—*Geologic Distribution*

	?	LOWER MIOCENE				UPPER MIOCENE							MIO-CENE	PLIOCENE	
		Bridge Creek	Crooked River	Eagle Creek	Republic	Type Payette	Type Mascall	Upper Cedarville	Latah of Washington	Trout Creek	Austin and Tipton	Payette-Latah of Idaho		Pliocene of California	Pliocene of High Plains
<i>Acer chaneyi</i>		?				X	X	X	X	X	X	X			X
<i>Acer merriami</i>		X			X	X	X	X	X	X	X	X			
<i>Acer negundoides</i>		X				X	X	X	X	X	X	X			
<i>Acer osmonti</i>		X	X			X	X	X	X	X	X	X			
<i>Acer septilobatum</i>			X			X	X	X	X	X	X	X			
<i>Arbutus matthesii</i>			X			X	X	X	X	X	X	X			
<i>Betula lacustris</i>		?				X	X	X	X	X	X	X		?	
<i>Castanopsis convexa</i>		X	X		X	X	X	X	X	X	X	X			X
<i>Cercidiphyllum erenatum</i> ..		X				X	X	X	X	X	X	X			
<i>Cercocarpus antiquus</i>		X				X	X	X	X	X	X	X			
<i>Dryopteris idahoensis</i>						X	X	X	X	X	X	X			
<i>Juglans hesperia</i>						X	X	X	X	X	X	X			
<i>Juniperus sabinoides</i>						X	X	X	X	X	X	X			
<i>Ostemon simplex</i>	X	X	X			X	X	X	X	X	X	X			
<i>Ostrya oregoniana</i>			X			X	X	X	X	X	X	X			
<i>Picea lahontense</i>						X	X	X	X	X	X	X			
<i>Pinus knowltoni</i>			X			X	X	X	X	X	X	X			
<i>Pinus tetrafolia</i>						X	X	X	X	X	X	X			
<i>Platanus dissecta</i>		X				X	X	X	X	X	X	X			
<i>Prunus rustii</i>						X	X	X	X	X	X	X			
<i>Pseudotsuga masoni</i>						X	X	X	X	X	X	X			
<i>Ptelea miocenica</i>						X	X	X	X	X	X	X			
<i>Quercus browni</i>						X	X	X	X	X	X	X			

[illegible]

species which range from the Lower Miocene through the Upper Miocene. In view of the long range of so many species, it is possible that many more of the typical Upper Miocene species survived into the Pliocene of the same region. Notwithstanding the absence of Pliocene floras in this region there are 4 Weiser species which are elsewhere restricted to the Pliocene and 6 species whose nearest relatives are restricted to the Recent, as against 12 species restricted to the Upper Miocene. These summaries suggest the conclusion that the Weiser flora is somewhat younger than the Upper Miocene floras concerned. On the basis of present knowledge, lacking comparative Pliocene floras in the same region, it may be stated that from the distributional data of species the Weiser flora can be assigned to the uppermost Miocene or lowermost Pliocene.

In order not to over-emphasize the mere absence or presence of identical or related species in other fossil floras, it is essential to compare the dominant species of the Weiser flora with those of related floras. The twelve most abundant species in the Weiser collections, arranged in their order of dominance are: *Typha lesquereuxi*, *Quercus browni*, *Quercus simulata*, *Acer negundoides*, *Salix coalingensis*, *Juniperus sabinoides*, *Arbutus matthesii*, *Pseudotsuga masoni*, *Castanopsis convexa*, *Odostemon simplex*, *Platanus dissecta*, and *Fraxinus coulteri*. This group closely resembles the Trout Creek association, in which the narrow-leafed oaks, *Quercus simulata* and *Q. traini*, are most abundant and *Arbutus matthesii*, *Salix* sp., *Pseudotsuga masoni*, *Typha lesquereuxi* and 2 species of *Odostemon* are among the 13 dominants.¹ In the Upper Cedarville flora 5 of the 13 most abundant species² are among the Weiser dominants. Although the dominants of the Payette flora have never actually been enumerated, recent observations on the flora from Sucker Creek³ indicate that at least three of the most abundant species are also dominants in the Weiser flora, namely, *Quercus browni*, *Quercus simulata* (*Castanopsis consimilis*), and *Castanopsis convexa*. Two of the Weiser species, *Platanus dissecta* and *Quercus simulata* are also among the 11 dominants of the Mascall flora,⁴ and among the 8 dominants of the Austin-Tipton flora.⁵ The Latah flora is much less similar, being dominated mainly by species of *Sequoia*, *Taxodium*, poplars, birches, broad-leafed oaks, and chestnuts.

It is evident that from the combined evidence of numerical representation of species and of comparison of dominants, the Weiser flora most nearly resembles the Trout Creek and Upper Cedarville floras. There is also considerable, though less striking, resemblance to the Mascall, Payette, Austin-Tipton and Latah floras.

¹ MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 40, 1933.

² LaMotte, Carnegie Inst. Wash. Pub. No. 455, 1936.

³ Brooks, Annals Carnegie Mus., vol. 24, 285-291, 1935.

⁴ Chaney, Carnegie Inst. Wash. Pub. No. 349, 35, 37, 1925.

⁵ Oliver, Carnegie Inst. Wash. Pub. No. 455, 4, 1934.

From the ecological and climatological aspect these closely related Upper Miocene floras exhibit minor differences from the Weiser flora which may indicate slight differences in age. In the Trout Creek floras, the relative abundance of such mesic species as *Acer merriami*, *Acer scottiae*, *Betula lacustris*, and *Thuites* sp., indicates a more humid assemblage than is found in the Weiser flora. MacGinitie has presented convincing evidence that the rainfall required by the Trout Creek forest probably averaged about 40 inches annually.¹ In the Austin-Tipton flora the dominance of mesic types such as *Sequoia langsdorffii*, *Umbellularia oregonensis*, *Corylus macquarri*, and *Fagus pacifica* also indicates a more humid forest than the Weiser flora, requiring an average of about 39 inches of annual rainfall.² Both the Mascall and Payette floras are likewise of more mesic aspect, including as dominants *Sequoia langsdorffii* and a number of its mesic associates, which require a minimum of 30 inches of annual rainfall.³ The Latah flora is somewhat more mesic with a stipulated rainfall of between 30 and 40 inches annually.⁴ The flora from the Upper Cedarville formation seems only slightly more mesic than the Weiser assemblage, and has been estimated to require an annual rainfall of between 23.6 and 29.5 inches.⁵ In contrast to all but the Upper Cedarville flora, the Weiser flora is much less mesic and appears to require an annual rainfall of 20 to 25 inches, as pointed out on pages 96 to 98.

In order to interpret these ecological and climatological observations in terms of age relationships, reliance must be placed on the assumption, based on both palæontologic and petrographic evidence, that there was a progressive trend from mild, humid climate to cooler, semiarid conditions in western North America during the Tertiary period.⁶ The lower rainfall requirements of the Weiser flora as compared with those of other Upper Miocene floras, with the possible exception of the Upper Cedarville flora, substantiate the assignment, based on distribution of species, of uppermost Miocene or lowermost Pliocene age.

It is a fortunate circumstance that the stratigraphic relations in the Weiser area are clearly in line with the transitional Miocene-Pliocene age reference of the Weiser flora. It has been shown in the discussion above that on the basis of floral evidence the Weiser flora appears to be somewhat younger than several Upper Miocene floras from the same general region, among which the Payette flora is included. This flora has been collected from the Payette formation in the same region which has yielded the Weiser flora. The sediments from which the Weiser flora was obtained are separated from the Payette formation by 440 to 2185 feet of basalt and a distinct

¹ MacGinitie, Carnegie Inst. Wash. Pub. No. 416. 39, 1933.

² Oliver, Carnegie Inst. Wash. Pub. No. 455. 7, 1934.

³ Chaney, Carnegie Inst. Wash. Pub. No. 349. 43, 1925.

⁴ Berry, U. S. Geol. Surv. Prof. Pap. 154-H, 234, 1928.

⁵ LaMotte, Carnegie Inst. Wash. Pub. No. 455, 1936.

⁶ Chaney and Elias, Carnegie Inst. Wash. Pub. No. 476, 1936.

erosional unconformity. In other places there is an additional intervening series of rhyolites. Such relationships obviously indicate that the Weiser flora must be younger than the Payette flora. How much younger, unfortunately, is not easily inferred since it is difficult to compute the amount of time required for the outpouring of the lavas and the development of the erosional unconformity. An additional time interval must be added for the deposition of the sediments in which the Weiser flora occurs, which are at least 1000 feet thick. The time required for this combination of depositional and erosional features suggests that the assignment to the lowermost Pliocene, rather than uppermost Miocene, is at least not unreasonable.

Evidence derived from vertebrate remains found in the sediments above the upper series of the Columbia River basalt lends considerable weight to the assignment to lowermost Pliocene rather than to uppermost Miocene. Kirkham has summarized¹ the vertebrate evidence for the Pliocene to early Pleistocene age of the Idaho formation. A large vertebrate fauna recently collected from the Hagerman lake beds, which appear to be the eastward extension of the upper part of the Idaho formation in the Weiser area, is indicative of Upper Pliocene age.² Unfortunately, none of the vertebrates listed by Kirkham or Gazin are found at the low stratigraphic levels from which the writer's plant collections were obtained. In the region south of Weiser, however, Buwalda³ has reported the occurrence of *Hipparion* teeth in the Poison Creek formation, which occupies approximately the same stratigraphic position as do the beds from which plants were collected in the Weiser area. These teeth are of Lower Pliocene aspect. It is therefore apparent that all of the vertebrate evidence points toward a Pliocene or later age for the Weiser plant-bearing beds, and that the nearest associated vertebrates are Lower Pliocene.

SUMMARY

The Weiser flora has been collected from slightly indurated shales and tuffs which overlie unconformably the upper series of the Columbia River basalts in the vicinity of Weiser, which is situated in the Snake River basin of southwestern Idaho. The beds from which the plants were obtained have been variously referred to the Upper Payette, Poison Creek, and Lower Idaho formations. Forty-five species have been recognized, of which two are described as new. Nine species are not represented by material sufficiently well preserved to make specific determinations possible.

The flora is composed entirely of typically temperate genera, the majority of which are still living in western North America. Out of a total of 35 species which show striking similarities in leaf or seed characters to modern species, about 68.5 per cent are comparable to species now living west of

¹ Kirkham, Jour. Geol., vol. 39, No. 3, 229, 1931.

² Gazin, Oral communication, Dec. 1935.

³ Buwalda, Idaho Bur. Mines and Geol., Pamph. 5, 1923; Science, n.s., vol. 60, 572, 1924.

the Great Plains and about 42.8 per cent are comparable to species at present restricted to the Pacific states west of the Rocky Mountains. Of the remaining species, five have their nearest living equivalents in eastern and central United States, three in eastern Asia, one in Europe, and one in Mexico.

Disregarding the exotic species which have been eliminated from the Pacific states since late Tertiary time, the Weiser flora is essentially similar to the *Lithocarpus-Quercus-Arbutus* community and its associated communities of the inner Coast Ranges of California. These communities grow at present on the inner, less mesic borders of the redwood forest and are dominated by species whose fossil equivalents are likewise the dominants of the Weiser flora. The inferred climatic requirements of the Weiser flora are mild temperatures, dry summers, and an annual rainfall of between 20 and 30 inches. These conditions are in contrast to the more humid climates inferred for the earlier Miocene floras of the same general region, and to the cooler and more arid conditions which prevail in the region today.

From the combined evidence of stratigraphic distribution of species, comparison of dominant species with dominants of other floras, and comparison of climatic conditions with those of other floras, the Weiser flora is referred to the uppermost Miocene or lowermost Pliocene. Stratigraphic relationships and associated vertebrate remains appear to favor the reference to the lowermost Pliocene.

SYSTEMATIC DESCRIPTIONS

Genus DRYOPTERIS Adanson

Dryopteris idahoensis Knowlton

Dryopteris idahoensis Knowlton, U. S. Geol. Surv. Eighteenth Ann. Rept., pt. 3, 721, pl. 99, figs. 1, 2, 1898.

Specimens of this species were not encountered in the writer's collections. Berry has, however, reported a single specimen of it¹ in a collection made by Kirkham from the Alkali Creek locality, which is Locality 638 of the present report.

Occurrence—Alkali Creek, Locality 638.

Collection—U. S. Nat. Museum.

Genus EQUISETUM Linné

Equisetum sp.

Six well-preserved specimens of flattened stems, showing both nodes and internodes are referable to this genus. Sufficient material is wanting, however, to make a more definite determination.

The specimens are portions of what seem to have been rather long stems. They are clearly fluted by numerous, parallel longitudinal ridges and grooves. Sheaths are missing. Branch scars are present just below the nodes, and one specimen has a lateral branch attached. Very few aerial stems of *Equisetum* have been described or figured from the Upper Tertiary of the

¹ Berry, U. S. Geol. Surv., Prof. Pap. 185-E, 103, pl. 19, figs. 2, 3, 1934.

West. Chaney has described a doubtful species from the Eagle Creek,¹ and Knowlton has figured a series of underground stems and tubercles from the Latah.² The Weiser specimens can not be compared with any particular living species.

Occurrence—Hog Creek, Locality 635; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., Nos. 1150, 1151, 1152.

Genus PINUS Linné

Pinus knowltoni Chaney

Pinus knowltoni Chaney, Contr. Walker Mus., vol. 2, No. 5, 160, pl. 5, figs. 3, 4, 1920.

Only one of many specimens of detached needles shows a fascicle of three needles. This is clearly referable to the common Miocene species *Pinus knowltoni*, which has been reported from the Mascall, Payette, Trout Creek, and Eagle Creek floras of the western states. The three-needed fascicles of *Pinus* sp. from Sucker Creek, Idaho³ and from the Latah⁴ are probably of the same species. Mason⁵ has compared this species with the modern *P. attenuata* Lemmon of the Coast Ranges of California. On the basis of foliage alone, there is also a similarity to the three-needed fascicles of *P. radiata* Don., *P. cembroides* Zucc., or *P. ponderosa* Dougl.

Occurrence—Hog Creek, Locality 635; Cove Creek, Locality 637.

Collection—U. C. Mus. Palæobot., No. 1153.

Pinus tetrafolia Berry

Pinus tetrafolia Berry, U. S. Geol. Surv., Prof. Pap. 154-H, 238, pl. 49, fig. 6, 1929

A single specimen was found showing long, slender needles in a fascicle of four needles. It is difficult, on the basis of a single specimen, to be certain that this may not have been a variant of the three-needed *Pinus knowltoni* Chaney or of a five-needed species such as *P. latahensis* Berry⁶ from which one needle has been lost. Five-needed fascicles are more common in the western pines than the four-needed type. Of the former, *P. monticola* Don., *P. lambertiana* Dougl., *P. torreyana* Carr., and *P. flexilis* James are typical, while *P. cembroides* Zucc. var. *parryana* Voss. is representative of the latter.

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., No. 1154.

Pinus sp.

Unfortunately only a single specimen of this species was found. It appears to be a two-needed fascicle and is thus distinct from the other pine foliage encountered. It must be remembered, however, that the loss of needles from a complete fascicle after it is shed from the tree is not uncommon, so that this two-needed fascicle may very possibly be one of *Pinus knowltoni* Chaney from which a single needle has been lost.

¹ Chaney, Contr. Walker Mus., vol. 2, No. 5, 159, 1920.

² Knowlton, U. S. Geol. Surv., Prof. Pap. 140-A, 24, pl. 9, fig. 1; pl. 26, fig. 5; pl. 29, fig. 8, 1926.

³ Brooks, Annals Carnegie Mus., vol. 24, 281, pl. 4, figs. 2, 3, 1935.

⁴ Knowlton, U. S. Geol. Surv., Prof. Pap. 140-A, 26, pl. 8, fig. 9, 1926.

⁵ Mason, Carnegie Inst. Wash. Pub. No. 346, 148, 1927.

⁶ Berry, U. S. Geol. Surv., Prof. Pap. 154-H, 238, pl. 49, fig. 7, 1929.

It is significant, moreover, that the two-needed fascicle of pine foliage is not reported from any of the other late Tertiary deposits of the west. In the Pleistocene, however, of both Carpenteria¹ and the Tomales region² of California they are abundant. These are referred to either the modern *Pinus muricata* D. Don. or *P. radiata* Don. The only other western pine with which a comparison might be made is *P. contorta* Dougl., which characteristically has a two-needed fascicle.

Occurrence—North-South Highway, Locality 636.

Collection—U. C. Mus. Palæobot., No. 1155.

Genus PICEA Link.

***Picea lahontense* MacGinitie**

(Plate 1, fig. 2)

Picea lahontense MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 46, pl. 3, figs. 4, 6, 8, 1933.

Two complete fruits are identical with the fruit figured by MacGinitie, and fit his description perfectly.

In comparison with modern conifers at The New York Botanical Garden, these fruits were found to be identical in all details with the western *Picea engelmanni* (Parry) Engelm. (See Sheet No. 473, from the Wenatchee Mts., Kittitas County, Washington).

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., Plesiotype, No. 1156; No. 1157.

Genus PSEUDOTSUGA Carr.

***Pseudotsuga masoni* MacGinitie**

(Plate 1, fig. 3)

Pseudotsuga masoni MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 47, pl. 3, figs. 1-3, 1933.

This species is represented by four fruits which can not be distinguished, except for their somewhat smaller size, from those figured by MacGinitie.

The writer has examined the fruits of the western species of *Pinus*, *Picea*, *Tsuga*, *Pseudotsuga*, and *Abies* in the determination of these fruits. The closest similarity was to *Pseudotsuga taxifolia* (Lamb.) Britt. (Sheet No. 3471, The New York Botanical Garden) from California. On the basis of a similar comparison with *P. taxifolia*, it is probable that the Weiser form may be a close relative of, or identical with, the Pliocene *P. sonomensis* Dorf.³ It is likely that many of the detached needles, which are common in the Weiser collections, are referable to *Pseudotsuga masoni*.

Occurrence—Hog Creek, Locality 635; Cove Creek, Locality 637.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1158; Nos. 1159, 1160.

Genus ABIES Link.

***Abies* sp.**

(Plate 1, fig. 6)

This genus is represented by a single cone scale, which is complete except for a small portion of the apex. The impression is of the inner side of the scale, showing the cavities left by the seeds at the base.

¹ Mason, Carnegie Inst. Wash. Pub. No. 415, 55, 1934.

² Mason, *op. cit.*, page 147, 1934.

³ Dorf, Carnegie Inst. Wash. Pub. No. 412, 72, 1930.

Tertiary species of *Abies* are comparatively rare. Mason, who has reviewed the fossil record of western conifers, records three species from the Mascall Miocene and one from the Crooked River Oligocene.¹ Only two of these, *A. chaneysi* Mason and *A. magnifica* var. *shastensis* Lemmon, are represented by scale impressions. In both of these, the scales were apparently of a much broader type than in the Weiser specimen.

In comparisons with modern types, it seemed advisable to compare this scale with those of *Pseudotsuga*, *Pinus*, *Picea*, *Tsuga*, and *Abies*. All of the western species of these genera were consulted at The New York Botanical Garden. By gradual elimination, it became certain that the reference to *Abies* was justified. The best comparison was with *Abies amabilis* (Sheet No. 7583, Olympic Mts., 4500 feet), in which the scale was identical with the Weiser specimen except for a slightly broader width.

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., Plesiotype, No. 1161.

Genus SEQUOIA Endl.

Sequoia langsdorfii (Brnt.) Heer

Sequoia langsdorfii (Brnt.) Heer, Fl. Tert. Helv., vol. 1, 54, pl. 20, fig. 2; pl. 21, fig. 4, 1855.

This species occurs only rarely in the Weiser collections.

In the absence of cones and inflorescences, it is extremely difficult to distinguish between fossil species of *Sequoia*, *Taxus*, and *Taxodium*.² In a study of these three genera at The New York Botanical Garden it was noted that the decurrent spiral leaves of *Sequoia* are always attached to the twig by a twisting of the entire width, and that the scale-leaves at the juncture of small and larger twigs are quite large, elongated, and conspicuously pointed. These diagnostic features are clearly seen in the Weiser specimens.

The specimens from Idaho are equally indistinguishable from the modern *Sequoia sempervirens* Endl. and *S. langsdorfii* from the Bridge Creek³ and the Latah.⁴

Occurrence—Hog Creek, Locality 635; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., Nos. 1162, 1163.

Genus LIBOCEDRUS Endl.

Libocedrus sp.

(Plate 1, fig. 4)

Three specimens of a type of seed quite different from the others in the collections are referable to this genus. Comparisons with herbarium specimens at The New York Botanical Garden indicate a close resemblance to the seeds of the living western species *Libocedrus decurrens* Torr. Unfortunately the writer did not obtain any specimens of leafy twigs of *Libocedrus* at any of the localities, though they have been previously reported by Berry⁵ from the same locality as the seeds here discussed.

The seeds from the Mascall formation which Mason⁶ has referred to the modern species *Libocedrus decurrens* are comparable to the Weiser speci-

¹ Mason, Carnegie Inst. Wash. Pub. No. 346, 149-151, 1927.

² Mason, Carnegie Inst. Wash. Pub. No. 346, 152, 1927.

³ Mason, *op. cit.*, pl. 5, figs. 4, 8.

⁴ Knowlton, U. S. Geol. Surv., Prof. Pap. 140-A, 26, pl. 9, figs. 3-6, 1926.

⁵ Berry, U. S. Geol. Surv., Prof. Pap. 185-E, 104, 1934.

⁶ Mason, Carnegie Inst. Wash. Pub. No. 346, 155, 1927.

mens but do not resemble them as closely as do the seeds of the living species. Other records of *Libocedrus* seeds are lacking, though there are several occurrences of leaf species, such as *L. prae-decurrens* Knowlton from the Latah,¹ and *Libocedrus* sp., from the Pliocene of California,² which from their close resemblance to the modern species are apparently closely related to, if not identical with, the Weiser species.

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1164; Nos. 1165, 1166.

Genus THUYA Linné

Thuya garmani Lesquereux

(Plate 1, fig. 1)

Thuya garmani Lesquereux, U. S. Geol. and Geog. Surv. Terr., Ann. Rept. (1872), 372, 1873.

Specimens of this species are rare but extremely well preserved at Locality 635. The generic reference to *Thuya* was made after a careful study of many twigs of *Thuya*, *Chamaecyperis*, *Libocedrus*, and *Cupressus* at The New York Botanical Garden. The specific reference is made on the basis of Mason's comparison of Miocene Elko and Mascall specimens with the modern *Thuya plicata* Don.,³ from which the Weiser specimens are not distinguishable.

The flat twig shown on Plate 1, figure 1, clearly shows the unlike pairs of short, rounded scales in whorls of four. In the Miocene *Libocedrus prae-decurrens* Knowlton⁴ and the modern *L. decurrens* Torr., the scales are consistently longer, the lateral scales have practically parallel inner edges which rarely meet at their bases, and the scales between the laterals are quite acutely pointed. In the closely similar twigs of *Chamaecyperis* all the scales are decidedly more acutely pointed and the lateral scales come together at their bases. It is also significant that in all the species of *Chamaecyperis* the twigs tend toward roundness rather than flatness as in *Thuya*.

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1167; No. 1168.

Genus JUNIPERUS Linné

Juniperus sabinoidea Ashlee

Juniperus sabinoidea Ashlee, Northwest Science, vol. 6, No. 2, 78, pl. 1, fig. 1, 1932.

About a half dozen well-preserved twigs with small, closely appressed leaves, apparently in whorls of three, are closely similar to the form described by Ashlee, although his figure is a poor one for a comparison of details.

An examination of modern herbarium material showed that these specimens are equally similar to the twigs of *Juniperus californica* Carr. and the common western *J. occidentalis* Hook., which are said to be indistinguishable on the basis of leaf characters.⁵

Occurrence—Hog Creek, Locality 635; North-South Highway, Locality 636.

Collection—U. C. Mus. Palæobot., Nos. 1169, 1170, 1171.

¹ Knowlton, U. S. Geol. Surv., Prof. Pap. 140-A, 28, pl. 8, fig. 8, 1926.

² Dorf, Carnegie Inst. Wash. Pub. No. 412, 74, 1930.

³ Mason, Carnegie Inst. Wash. Pub. No. 346, 155, 1927.

⁴ Knowlton, U. S. Geol. Surv., Prof. Pap. 140-A, 28, pl. 8, fig. 8, 1926.

⁵ Jepson, *Manual of the Flowering Plants of California*, 59, 1925.

Genus *TYPHA* Linné*Typha lesquereuxi* Cockerell

Typha lesquereuxi Cockerell, Bull. Torr. Bot. Club, vol. 33, 307, 1906.

A large number of specimens of fragmentary leaves are indistinguishable from the figured specimens of this wide-spread Tertiary species. Although well-defined characteristics are lacking, there is a general resemblance to the linear, parallel-veined leaves of the modern *Typha latifolia* Linné, which is wide-spread in the temperate regions of the northern hemisphere.

Occurrence—Hog Creek, Locality 635; North-South Highway, Locality 636; Cove Creek, Locality 637; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., No. 1172.

Genus *CYPERACITES* Schimper*Cyperacites* sp.

There are several small fruits in the Weiser collections which Dr. H. L. Mason of the University of California has identified as belonging to the sedge family, showing a similarity to the fruits of such genera as *Carex* and *Cyperus*. The Weiser specimens are essentially similar to fruits referred to *Cyperacites* sp., from the High Plains flora of Oklahoma.¹

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., No. 1173.

Genus *SALIX* Linné*Salix coaligensis* Dorf

Salix coaligensis Dorf, Carnegie Inst. Wash. Pub. No. 412, 78, pl. 7, figs. 5-7; pl. 8, figs. 1, 2, 1930.

Eight specimens from four localities are sufficiently well preserved to make a definite determination. All the characters of shape, venation, margin, tip, and base are essentially identical with those of the Pliocene specimens.

As mentioned in the original discussion of *Salix coaligensis*, the closest modern correlatives seem to be *S. lasiolepis* Benth. and *S. lasiandra* Benth.

Occurrence—Hog Creek, Locality 635; North-South Highway, Locality 636; Cove Creek, Locality 637; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., No. 1174.

Genus *JUGLANS* Linné*Juglans hesperia* Knowlton

Juglans hesperia Knowlton, U. S. Geol. Surv., Eighteenth Ann. Rept., pt. 3, 723, pl. 99, fig. 8, 1898.

Six incomplete but well-preserved specimens are indistinguishable from the figured Payette specimen of this species.

In his recent report on the Trout Creek flora² MacGinitie placed this species in synonymy with *Juglans oregoniana* Lesquereux, which LaMotte has subsequently referred to *Carya egregia* (Lesq.) LaMotte³ on rather convincing evidence. The writer is in agreement with this determination for the majority of specimens of *Juglans oregoniana*, but feels that the cordate base, the high angle of divergence of the secondaries, the enlarged

¹ Chaney and Elias, Carnegie Inst. Wash. Pub. No. 476, 1936.

² MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 50, 1933.

³ LaMotte, Carnegie Inst. Wash. Pub. No. 455, 1936.

base, and the fine marginal serrations of the Payette and Weiser specimens are sufficiently different from those characters in *Carya egregia* to be the basis of a distinct species. The combination of observed characters appears to relate the species more closely to *Juglans* than to *Carya*.

The leaves here referred to *Juglans hesperia* are practically identical with those of *J. nigra* Linné, of the eastern and central United States.

Occurrence—Cove Creek, Locality 637; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., Nos. 1175, 1176.

Genus *OSTRYA* Scop.

Ostrya oregoniana Chaney

(Plate 2, fig. 10)

Ostrya oregoniana Chaney, Carnegie Inst. Wash. Pub. No. 346, 106, pl. 9, fig. 12; pl. 10, figs. 1-4, 1927.

Only three specimens from one locality are referable to this species. Chaney points out in his original description of the species that the leaves can not easily be distinguished from those of *Carpinus grandis* Unger. In the Weiser specimens the well-developed tertiary veins which connect with marginal teeth, the character of the marginal teeth, and the general shape of the leaf indicate a closer similarity to the figured specimens of *Ostrya oregoniana*. It is unfortunate that seeds were not found to corroborate the determination.

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1177.

Genus *BETULA* Linné

Betula lacustris MacGinitie

(Plate 1, fig. 5)

Betula lacustris MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 50, pl. 4, figs. 2, 3, 4, 1933.

Several incomplete leaves in the Weiser collections are referable to this species. Also, in close association, are three specimens of small winged nutlets which are identical with the fruits of the modern *Betula fontinalis* Sarg. In view of MacGinitie's correlation of the leaves of *B. lacustris* with *B. fontinalis*, with which the writer's studies are in agreement, it seems unreasonable to describe the Weiser fruits as a new species.

Description—Complete fruits 2 to 2½ mm. long, 3 to 5 mm. wide; nutlets fusiform, widest at the middle, tufted at top by two long, delicate styles; wings broad, each one generally about twice as broad as the nutlet.

In comparisons with modern species, all available species of *Betula* and *Alnus* were consulted at The New York Botanical Garden. In all the fruits of *Alnus*, the wings were invariably much narrower in proportion to the nutlet than was true in *Betula*.

The Weiser fruits of this species are quite similar except in their smaller size, to the one figured by Berry from the Latah,¹ and are of essentially the same type as the fruit of *Betula heterodonta* Newb., from the Bridge Creek.²

Occurrence—Hog Creek, Locality 635; Cove Creek, Locality 637.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1178; No. 1179.

¹ Berry, U. S. Geol. Surv., Prof. Pap. 154-H, 244, pl. 63, fig. 9, 1929.

² Newberry, U. S. Geol. Surv. Mon. 35, 65, pl. 45, fig. 6, 1898.

Genus *ALNUS* Hill.*Alnus* sp.

Three fairly complete specimens from Locality 637 and one from Locality 638 are clearly referable to the genus *Alnus*. It is somewhat more difficult to be certain of the specific determination. The specimens are more similar to the leaves of the modern *Alnus rubra* Bong., than to any fossil specimens which have been figured. The common Miocene species *A. carpinoides* Lesquereux is quite distinct, resembling closely the living *A. tenuifolia* Nutt. and *A. sinuata* Rydb. in the majority of its characteristics.¹ In a recent paper LaMotte² suggests a resemblance also to *A. rubra*, pointing out that *A. carpinoides* may be the undifferentiated ancestral type of all three of the living species.

It is possible that the Weiser species may be closely related or similar to *Alnus merriami* Dorf from the California Pliocene³ and an unfigured *Alnus* sp. from the Mascall,⁴ since both of these are said to resemble the modern *A. rubra*. Lacking complete specimens in the Weiser collections, however, the writer feels it advisable to make only a provisional determination at the present time.

Occurrence—Cove Creek, Locality 637; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., Nos. 1180, 1181, 1182.

Genus *CASTANOPSIS* Spach.*Castanopsis convexa* (Lesq.) Brooks

(Plate 1, figs. 7, 8)

Castanopsis convexa (Lesq.) Brooks, *Annals Carnegie Mus.*, vol. 24, 288, pl. 6, fig. 5; pl. 10, figs. 1, 3; pl. 12, figs. 1-6; pl. 13, figs. 4-6; pl. 18, figs. 3-5; pl. 20, fig. 4; pl. 21, fig. 1-b, 1935.

This species is fairly abundant in the Weiser collections and is represented by well-preserved specimens, which are essentially similar to those figured from the Sucker Creek flora.

The long list of synonymous species tabulated by Mrs. Brooks conveys the correct impression that leaves of this type are quite abundant in the late Tertiary deposits of the West. Whether or not the entire synonymy will survive more complete scrutiny remains to be seen. At any rate, the reference to *Castanopsis*, based on the combined evidence of shape, size, margin, and primary, secondary, and tertiary venation seems a reasonable one, though still lacking the corroborative evidence of attached fruits.

Among modern species, the closest resemblance in the leaf forms of *Castanopsis convexa* seems to be with *C. sempervirens* Dudley. The closely related *C. chrysophylla* A. DC. has uniformly longer, more lanceolate leaves with acute or acutely elongated tips.

Occurrence—Hog Creek, Locality 635; North-South Highway, Locality 636; Cove Creek, Locality 637.

Collection—U. C. Mus. Palæobot., Plesiotypes Nos. 1183, 1184; Nos. 1185, 1186, 1187.

¹ Chaney, *Carnegie Inst. Wash. Pub. No. 349*, 7-10, 1925.

² LaMotte, *Carnegie Inst. Wash. Pub. No. 455*, 1936.

³ Dorf, *Carnegie Inst. Wash. Pub. No. 412*, 80, pl. 8, figs. 6, 7, 1930.

⁴ Chaney, *Carnegie Inst. Wash. Pub. No. 349*, 26, 40, 1925.

Genus QUERCUS Linné

Quercus browni Brooks

(Plate 2, fig. 3)

Quercus browni Brooks, Annals Carnegie Mus., vol. 24, 291, pl. 14, figs. 3-8, 1935.

This species is extremely abundant in the Weiser flora and is fortunately represented by well-preserved, complete specimens. The reference to *Q. browni* was made after considerable hesitancy, in view of the similarity of the Weiser specimens to *Q. traini* MacGinitie of the Trout Creek flora¹ and *Q. hannibali* Dorf of the California Pliocene.² Both of these species, as well as *Q. browni* from both Sucker Creek and Weiser, appear to be closely similar in leaf forms to the modern *Q. chrysolepis* Liebm. There is also an undescribed Payette species which Chaney correlates with *Q. chrysolepis*.³

Such a large number of species which are obviously closely related to a single modern species which, moreover, possesses an extremely variable leaf form, makes it difficult to make an accurate determination on the basis of a few fossil specimens. The Weiser specimens, however, are essentially identical with the figured specimens of *Q. browni*, and differ in minor, but perhaps important, details from *Q. traini* and *Q. hannibali*. At The New York Botanical Garden, moreover, it was found possible to duplicate each of the Weiser specimens in the various herbarium sheets of *Q. chrysolepis*.

Despite the aforementioned difficulties in determinations, it is apparent that the *Q. chrysolepis* type of oak is one of the most wide-spread and abundant in western Miocene and Pliocene floras.

Occurrence—Hog Creek, Locality 635; North-South Highway, Locality 636; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1188; Nos. 1189, 1190.

Quercus cognata Knowlton

(Plate 2, fig. 1)

Quercus cognata Knowlton, U. S. Geol. Surv., Prof. Pap. 140-A, 36, pl. 20, figs. 1-4; pl. 21, figs. 1, 2, 1926.

Several specimens, one of which is virtually complete, show a combination of characters which individually have previously been regarded as of specific importance. In general size, shape, and marginal characters the Weiser specimens are more like *Quercus payettensis* Knowlton⁴ than any other species. The slender, acuminate tips of the leaves, however, are much more similar to those of the closely related *Q. rustii* Knowlton,⁵ or *Q. merriami* Knowlton.⁶ Berry has pointed out⁷ that all three of these species are probably variants of the abundant Latah species *Q. cognata*. He does not, however, combine them as synonymous with the latter.

In the opinion of the writer, it seems inadvisable to retain such variants as distinct species, since this involves the description of additional new species every time another variant is discovered which does not agree precisely with the published descriptions or figures of the nominal species mentioned above. For this reason, the Weiser specimens have been referred

¹ MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 53, pl. 5, figs. 1, 2, 1933.² Dorf, Carnegie Inst. Wash. Pub. No. 412, 86, pl. 8, figs. 8-11, 1930.³ Chaney, Amer. Jour. Sci., vol. 4, 219, 1922.⁴ Knowlton, U. S. Geol. Surv., Prof. Pap. 140-A, 37, pl. 21, figs. 5-7, 1926.⁵ Knowlton, *op. cit.*, 36, pl. 21, figs. 3, 4.⁶ *Idem*, page 35, pl. 19, figs. 4, 5.⁷ Berry, U. S. Geol. Surv., Prof. Pap. 185-E, 109, 1934.

to the better known and more common species *Q. cognata*. Chaney has written to the writer that leaves of this type have recently been found to be numerous in an undescribed Miocene flora from Nevada County, California.

Among modern western oaks *Q. cognata* bears a close resemblance to *Q. morehus* Kell., which is commonly considered to be a hybrid between *Q. kelloggii* Newb. and *Q. wislizenii* A. DC. It differs from *Q. kelloggii* only in possessing shallower sinuses and entire lobes, each of which is terminated in a single pointed tooth. The resemblance to *Q. wislizenii* is more remote.

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1191.

Quercus declinata Dorf

(Plate 2, fig. 2)

Quercus declinata Dorf, Carnegie Inst. Wash. Pub. No. 412, 88, pl. 8, figs. 12, 13, 1930.

Three fairly complete specimens are referred to this species, which the writer has compared with the modern *Quercus tomentella* Engelm. In the shape of the marginal teeth and in the parallel venation, there is a superficial resemblance to *Lithocarpus predensisflora* Brooks from the Sucker Creek flora.¹ This, however, like its modern correlative, *L. densiflora* (H. & A.) Rehd., is distinctly more lanceolate than the Weiser specimens. The same similarities and differences are apparent in a comparison with *Q. klamathensis* MacGinitie from the Trout Creek flora.²

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1192.

Quercus duriuscula Knowlton

(Plate 2, fig. 8)

Quercus duriuscula Knowlton, U. S. Geol. Surv., Bull. 204, 50, pl. 8, fig. 2, 1902.

Five specimens in the collections are clearly of this type of oak, differing only from the figured type specimen in the smaller size of the secondary lobes and a slightly less obovate shape. The general size, venation, base, apex, and character of the rounded lobes are identical with the Mascall specimen.

Chaney has reported³ that this species is fairly common in the Mascall flora and has pointed out its close resemblance to *Q. columbiana* Chaney from the Eagle Creek flora.⁴ Among modern species the Weiser specimens show a closer similarity to *Q. garryana* Dougl. than to any other western species. There is also a superficial resemblance to the eastern *Q. alba* Linné.

Occurrence—Cove Creek, Locality 637.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1193; No. 1194.

Quercus mccanni Berry

Quercus mccanni Berry, U. S. Geol. Surv., Prof. Pap. 170-C, 36, pl. 11, figs. 5-7, 1931.

A single, almost complete specimen and several fragments are referred to this species. The Weiser specimens differ from the figured specimens of

¹ Brooks, *Annals Carnegie Mus.*, vol. 24, 290, pl. 14, fig. 1, 1935.

² MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 52, pl. 5, fig. 3, 1933.

³ Chaney, Carnegie Inst. Wash. Pub. No. 349, 26, 1925.

⁴ Chaney, Walker Mus. Contr., vol. 2, No. 5, 170, pl. 13, figs. 1, 2, 1920.

Quercus mccanni only in having two of the secondary veins branched near the margin, each branch terminating in blunt marginal teeth.

This unusual type of oak leaf is compared by Berry to the chestnut-oaks of southeastern North America. There does not seem to be a closely related leaf form in any of the western species.

Occurrence—North-South Highway, Locality 636; Cove Creek, Locality 637.

Collection—U. C. Mus. Palæobot., Nos. 1195, 1196.

Quercus simulata Knowlton

(Plate 1, figs. 9, 10)

Quercus simulata Knowlton, U. S. Geol. Surv., Eighteenth Ann. Rept., pt. 3, 728, pl. 101, figs. 3, 4; pl. 102, figs. 1, 2, 1898.

Quercus consimilis MacGinitie (not Newberry), Carnegie Inst. Wash. Pub. No. 416, 52, pl. 5, fig. 5; pl. 6, figs. 1, 5, 6, 8, 1933.

A large number of specimens in the Weiser collections can be referred to this species, whose status is still in a somewhat confused state.

In her report on the Sucker Creek flora, Mrs. Brooks recently presented evidence for the inclusion of *Quercus simulata*, *Q. consimilis*, and several other species in the new combination, *Castanopsis consimilis*.¹ In a more recent publication, and evidently unaware of Mrs. Brooks' work, LaMotte² has pointed out a number of differences between the typical leaves of *Quercus simulata* and *Q. consimilis*, based on studies which he and MacGinitie made on type material of both species. The writer is consequently faced with two alternatives: referring the Weiser species either to *Castanopsis consimilis* or to *Quercus simulata*.

Since the writer agrees with LaMotte that there are recognizable differences between the leaves of the Lower Miocene *Quercus consimilis* and the Upper Miocene *Q. simulata*, and since the Weiser specimens are clearly of the latter type, it seems advisable to refer them to *Q. simulata*. It is felt by the writer that the long list of synonymous species given by Mrs. Brooks contains several species, including those above and *Castanea orientalis*, which can under normal circumstances readily be differentiated. It is possible that the reference to *Castanopsis* rather than to *Quercus* is correct. Her basis for such reference, namely the minute details of the tertiary venation, is, however, rather unfortunate, since it does not seem to be an easily recognizable character and is often not well preserved in fossil specimens.

The well-defined characters of the Weiser specimens closely resemble those of *Quercus myrsinæfolia* Blume, which both MacGinitie³ and LaMotte⁴ regard as the living species most similar to the Trout Creek and Upper Cedarville specimens of *Q. simulata*.

Occurrence—Hog Creek, Locality 635; North-South Highway, Locality 636; Cove Creek, Locality 637; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., Plesiotypes Nos. 1197, 1198; Nos. 1199, 1200.

¹ Brooks, *Annals Carnegie Mus.*, vol. 24, 285, 1935.

² LaMotte, *Carnegie Inst. Wash. Pub. No. 455*, 1936.

³ MacGinitie, *Carnegie Inst. Wash. Pub. No. 416*, 52, pl. 5, fig. 4, 1933.

⁴ LaMotte, *Carnegie Inst. Wash. Pub. No. 455*, 1936.

Genus ULMUS Linné

Ulmus moorei Chaney

(Plate 2, fig. 4)

Ulmus moorei Chaney, Carnegie Inst. Wash. Pub. No. 476, 1936.

This species is represented in the Weiser collections by five well-preserved leaf specimens and several fragments of leaves. These are clearly of the small, broad, simple-serrate types which Chaney has recently described from the High Plains Pliocene. They are equally comparable to the small elm leaves from the California Pliocene¹ which were referred to *Ulmus brownellii*, but which Chaney has since included in *Ulmus moorei*. The basis for separation from *U. brownellii* is chiefly their consistently smaller size and broader width.

In addition to leaf specimens, there are also three well-defined fruits in the collections which are unmistakably referable to *Ulmus*. In view of the occurrence of two leaf species, but only one type of fruit in the Weiser flora, it is obvious that the fruits might well belong to either of the leaf species, *Ulmus moorei* or *U. speciosa*. In comparison with previously known elm fruits, it is apparent that the Weiser fruits are distinctly not of the *speciosa* type,² but resemble closely the fruits of the *brownellii* type,³ differing mainly in the narrower wing and relatively larger size of the seed. This resemblance strongly suggests that the Weiser fruits belong to the leaves of *Ulmus moorei*, since they likewise differ only in minor details from the leaves of *U. brownellii*.

Among modern species the leaves and fruits of *Ulmus moorei* resemble those of the Japanese species, *U. parvifolia* Jacq., particularly where it grows under somewhat xeric conditions.

Occurrence—Hog Creek, Locality 635; North-South Highway, Locality 636; Cove Creek, Locality 637; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1201; Nos. 1202, 1203.

Ulmus speciosa Newberry

Ulmus speciosa Newberry, U. S. Nat. Mus. Proc., vol. 5, 507, 1883; U. S. Geol. Surv., Mon. 35, 80, pl. 45, figs. 3, 4, 7, 1896.

Along with the fruits and small, simple-serrate leaves referred to *Ulmus moorei* there are three leaves which are unmistakably similar to the larger, narrower, and double-serrate leaves of *Ulmus speciosa*. This species resembles the living *U. americana* Linné of eastern North America and to some degree the European species, *U. montana* With.⁴ There are no fruits in the collections which can be referred to this species.

The poor representation of this species in both numbers and local distribution is suggestive of conditions which were not sufficiently mesic to permit more than a limited growth. This conclusion is amply corroborated by the somewhat xeric nature of the Weiser flora as a whole.

Occurrence—Cove Creek, Locality 637.

Collection—U. C. Mus. Palæobot., No. 1204.

¹ Dorf, Carnegie Inst. Wash. Pub. No. 412, 92, pl. 10, figs. 1, 2, 3, 10, 1930.

² Chaney, Carnegie Inst. Wash. Pub. No. 346, 114, pl. 12, fig. 5, 1927.

³ Chaney, *op. cit.*, page 113, pl. 13, fig. 4.

⁴ Chaney, Carnegie Inst. Wash. Pub. No. 346, 114, 1927.

Genus *PLATANUS* Linné*Platanus dissecta* Lesquereux

Platanus dissecta Lesquereux, Mem. Mus. Comp. Zool., vol. 6, No. 2, 13, pl. 7, fig. 12; pl. 10, figs. 4, 5, 1878.

About a dozen specimens are referable to this common Miocene species. They present the same characteristics of shape, size, venation, margin, and variability as are shown in the specimens from the Latah¹ and Sucker Creek² floras. The specimens were also compared and found to be identical with those of *P. dissecta* in the Princeton University collections from the Mascall.

In addition to leaves, the Weiser collection also has two specimens which are unquestionably the stipules of *Platanus*, similar to those reported from the Austin-Tipton flora.³ At The New York Botanical Garden, these stipules were compared with modern species and found to be very similar to those of *P. occidentalis* Linné (see Sheet No. 1899, Watchung, New Jersey). There appear to be integrated variations between the typical *P. occidentalis* leaf and the typical *P. racemosa* leaf, making it difficult to compare the fossil species, *P. dissecta*, with one or the other. The writer's observations indicate a closer similarity to the leaves of *P. racemosa* in the less arid portions of its range.

Occurrence—Hog Creek, Locality 635; Cove Creek, Locality 637; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., Nos. 1205, 1206, 1207.

Genus *CERCIDIPHYLLUM* Siebold and Zuccarini*Cercidiphyllum crenatum* (Unger) Brown

(Plate 2, fig. 9)

Cercidiphyllum crenatum (Unger) Brown, Jour. Paleon., vol. 9, No. 7, 575, pl. 68, figs. 1, 6, 8-10, 1935.

This species is represented by two incomplete leaves and a single seed. These are essentially similar to the leaves and seeds from the Bridge Creek shale and from Republic, Washington.

In view of the wide-spread occurrence of leaves of this type in Tertiary deposits of the west, it is gratifying to have their systematic status settled on such convincing evidence. Their former reference to *Grewia* and *Cassia* made it impossible to attempt any climatological or ecological inferences from their presence in floras of temperate aspect. Brown has shown the similarity between the leaves and seeds of this species to those of the living *Cercidiphyllum japonicum* Siebold and Zuccarini of the temperate forests of Japan and western China.

Occurrence—Hog Creek, Locality 635; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1208; Nos. 1209, 1210.

¹ Berry, U. S. Geol. Surv., Prof. Pap. 154-H, 248, pl. 53, figs. 1, 2; pl. 61, 1929.

² Brooks, Annals Carnegie Mus., vol. 24, 294, pl. 17, figs. 2, 3, 4; pl. 18, figs. 1, 2, 1935.

³ Oliver, Carnegie Inst. Wash. Pub. No. 455, 22, pl. 3, fig. 3, 1934.

Genus *ODOSTEMON* Rafinesque*Odostemon simplex* (Newb.) Cockerell

Berberis simplex Newberry, U. S. Geol. Surv., Mon. 35, 97, pl. 56, fig. 2, 1898.
Odostemon simplex (Newb.) Cockerell, Amer. Mus. Nat. Hist., Bull., vol. 24, 91, 1908.

Ten specimens in the Weiser collections are clearly referable to this species. Its occurrence at Locality 635 has been previously reported by Berry.¹

Several of the specimens are identical in all details with the specimens figured by Chaney from the Crooked River flora.² Others approximate the more rounded, less spinose form of the Pliocene *Q. hollicki*,³ and one specimen is of a very narrow, lanceolate leaflet of a type not previously recorded. All of the forms are regarded as probable variants of a single species, as similar leaves and variations were noted in herbarium sheets of the modern species *O. californica* Rydb., and to a lesser degree *O. fremontii* Rydb. at The New York Botanical Garden. It is of ecological significance to note that the Weiser specimens resemble these xeric species more closely than they do the mesic species, *O. nervosus* Rydb., which is commonly associated with the redwood in the more humid portions of the northern Coast Ranges.

Occurrence—Hog Creek, Locality 635; North-South Highway, Locality 636.

Collection—U. C. Mus. Palæobot., Nos. 1211, 1212, 1213.

Genus *PRUNUS* Linné*Prunus rustii* Knowlton

(Plate 2, fig. 6)

Prunus rustii Knowlton, U. S. Geol. Surv., Prof. Pap. 140-A, 43, pl. 24, figs. 4, 5, 1926.

One specimen and its counterpart are indistinguishable from this Latah species. A single crushed fruit possessing essentially, except for its smaller size, the same characters as the figured specimen of *Prunus coveus* from the Crooked River⁴ was also found.

Among modern species, the Weiser specimens were closely comparable to herbarium specimens of *P. demissa* studied at The New York Botanical Garden.

Occurrence—Hog Creek, Locality 635; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1214; No. 1215.

Genus *CERCOCARPUS* H. B. K.*Cercocarpus antiquus* Lesquereux

Cercocarpus antiquus Lesquereux, Mus. Comp. Zool., Mem., vol. 6, pt. 2, 37, pl. 10, figs. 6-11, 1878.

Only two leaf specimens are referable to this species. These are quite obovate-lanceolate in shape, with straight, prominent secondaries, distinctly cuneate base, and entire margins, paralleling the secondaries, to the middle of the leaf, above which they are marked by coarse teeth at the ends of each secondary; the tip is not preserved.

¹ Berry, U. S. Geol. Surv., Prof. Pap. 185-E, 112, 1934.

² Chaney, Carnegie Inst. Wash. Pub. No. 346, 116, pl. 14, figs. 7, 8, 9, 11, 1927.

³ Dorf, Carnegie Inst. Wash. Pub. No. 412, 93, pl. 10, figs. 7, 8, 1930.

⁴ Chaney, Carnegie Inst. Wash. Pub. No. 346, 123, pl. 15, fig. 2, 1927.

In addition to the Table Mountain occurrence, this species is also recorded from several localities of the Mascall Miocene.¹ It differs from the Pliocene *C. cuneatus*² in being more lanceolate and considerably larger. Among modern species, the Weiser forms show the closest resemblance to the more lanceolate leaflets often exhibited in *C. betuloides* Nutt.

Occurrence—Cove Creek, Locality 637.

Collection—U. C. Mus. Palæobot., No. 1216.

Genus LEGUMINOSITES Bowerbank

Leguminosites sp.

(Plate 3, fig. 1)

A single well-preserved pod was found at Locality 635. It is exactly 3.5 cm. long and 1 cm. wide at its widest portion just above the middle; the apex is poorly preserved but appears to have been obtusely pointed; the base is abruptly broken across; within the pod, near the base, are five ovoid dots in a row, possibly representing immature seeds.

It has not been possible to refer this pod to a definite genus. While showing a superficial resemblance to *Cercis*, there is also similarity to the pods of *Robinia* and *Lathyrus*. There do not seem to be any described or figured Tertiary forms with which the Weiser specimen can be compared. Chaney, however, reports³ that he has a pod from the Bridge Creek flora which is almost identical with it.

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1217.

Genus PTELEA Linné

Ptelea miocenica Berry

(Plate 2, figs. 5, 7)

Ptelea miocenica Berry, U. S. Geol. Surv., Prof. Pap. 170-C, 39, pl. 12, fig. 7, 1931.

Several circular samaras which are referable to the genus *Ptelea* were found at Locality 635. The complete samaras average about 1.5 cm. in diameter. The central seed is subcircular and about 1.6 cm. in diameter. The peduncle is incompletely preserved beyond the margin, but is clearly split within the margin into three divisions. The wings are extremely thin and clearly marked by reticulate veins. Their outer margins are imperfectly preserved, making it impossible to determine whether they are entire or fringed.

The characters of these samaras clearly relate them to *Ptelea miocenica*, which, in addition to the Grand Coulee occurrence cited above, is reported from the Trout Creek⁴ and Upper Cedarville⁵ floras. There are no leaves in the Weiser collections which can be referred to this species. Their absence may in part be explained by the somewhat xeric conditions indicated by the flora as a whole. Under such conditions the leaves are subject to drying and possibly complete crumbling before or during transportation toward basins of deposition. Fruits, on the other hand, are better adapted to

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. 2, 30, 33, 36, 1925.

² Dorf, *op. cit.*, No. 412, 98, pl. 12, fig. 3, 1933.

³ Chaney, Written communication, Sept. 3, 1935.

⁴ MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 59, pl. 11, fig. 1, 1933.

⁵ LaMotte, Carnegie Inst. Wash. Pub. No. 455, 1936.

withstand such conditions and are often, as in the case of these samaras, specifically adapted to wide dispersal by wind and water currents.

Among modern species, these samaras are close to those of *Ptelea trifoliata* Linné of eastern and central North America.

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., Plesiotypes Nos. 1218, 1219.

Genus CELASTRUS Linné

Celastrus sp.

(Plate 3, fig. 7)

Only a single specimen of this type was encountered in the collections. The reference to *Celastrus* was made after considerable difficulty in attempting to discover modern leaves with the characteristics shown. The closest similarity, as determined by Dr. R. W. Chaney, was with *Celastrus pringlei* Rose,¹ which grows in the canyons of the mountains above Cuernavaco, Mexico, at an altitude of 7500 feet. Chaney has informed the writer that it grows there in association with typical temperate genera, many of which are represented in Miocene floras of western America.

The writer has not seen any Tertiary species which is comparable to the Weiser specimen.

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1220.

Genus ACER Linné

Acer chaneyi Knowlton

Acer chaneyi Knowlton, U. S. Geol. Surv., Prof. Pap. 140-A, 45, pl. 27, fig. 2, 1926.

Acer gigas Knowlton, U. S. Geol. Surv., Bull. 204, 76, pl. 14, fig. 1, 1902.

A single specimen of an extremely large maple fruit is referable to the nominal species, *A. gigas*, which MacGinitie regards as synonymous with the leaf species *A. chaneyi*, on the basis of the similarity of the leaf and large fruit to the living *A. saccharinum* Linné.² A similar large fruit is reported from the Sucker Creek flora,³ in association with the *A. chaneyi* type of leaf.

The Weiser collections also contain three fairly complete leaf impressions which possess the long, slender, deeply cut lobes so characteristic of the leaf species. In view of this repeated association of leaves and fruits comparable to a single modern species, the writer feels no hesitancy in helping to simplify the literature by combining the fruits and leaves under one specific name as MacGinitie has done.

Occurrence—Hog Creek, Locality 635; North-South Highway, Locality 636; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., Nos. 1221, 1222, 1223.

Acer merriami Knowlton

(Plate 3, fig. 8)

Acer merriami Knowlton, U. S. Geol. Surv., Bull. 204, 76, pl. 16, fig. 7, 1902.

Acer oregonianum Knowlton, U. S. Geol. Surv., Bull. 204, 75, pl. 13, figs. 5-8, 1902.

A single, complete fruit is identical with the figured specimens of *Acer oregonianum* from the Mascall flora, which MacGinitie⁴ regards as probably

¹ Univ. Calif. Herbarium, Sheet No. 138168.

² MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 61, 1933.

³ Brooks, Annals Carnegie Mus., vol. 24, 297, pl. 19, fig. 5; pl. 21, fig. 1-a, 1935.

⁴ MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 61, pl. 10, fig. 1, 1933.

the fruits of *Acer merriami* on the basis of similarity to the modern *A. macrophyllum* Pursh. There is also a close resemblance, except for the rounded seed, to the fruits of *Acer osmonti* Knowlton from the Crooked River flora.¹

The *Acer* fruits from the Latah, which are referred to *A. oregonianum*,² seem to the writer of a distinctly different type, similar to *A. negundoides* MacGinitie of the Trout Creek flora.³

Unlike the Trout Creek occurrence, the Weiser fruits of this type are not found associated with any leaves of the *A. macrophyllum* type.

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1224.

Acer negundoides MacGinitie

(Plate 3, fig. 2)

Acer negundoides MacGinitie, Carnegie Inst. Wash. Pub. No. 416, pl. 11, figs. 2, 3, 1933.

About a dozen well-preserved and complete fruits are identical with the figured specimens from the Trout Creek flora. Except for their small size, the specimens are not unlike the figured specimens of *A. oregonianum* Knowlton from the Latah⁴ and *A. minor* Knowlton from the Mascall.⁵ Although Berry compares the Latah species with the modern *A. macrophyllum* Pursh and *A. circinatum* Pursh,⁶ the writer feels that MacGinitie's comparison with *A. negundo* Linné is a closer one.

There are no leaves in the collections which can be attributed to this species. As previously mentioned (p. 119) this may in part be due to the somewhat xeric conditions, which are not particularly conducive to leaf preservation.

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1225; Nos. 1226, 1227.

Acer osmonti Knowlton

Acer osmonti Knowlton, U. S. Geol. Surv., Bull. 204, 72, pl. 13, fig. 3, 1902.

Four incomplete but well-preserved leaf specimens are indistinguishable from one or another of the figured specimens of *A. osmonti* from the Bridge Creek or the Crooked River floras.⁷ All of the Weiser specimens are distinctly trinerved, with broad lobes quite unlike those of *A. chaneyi* Knowlton.

Among modern maples, Chaney has compared *A. osmonti* with *A. glabrum* Torr.,⁸ a similarity which has been very adequately borne out in the writer's comparisons of the Weiser specimens with herbarium material. In the absence of fruits of the *A. glabrum* type, it is possible that the fruits referred above to *A. negundoides* may have belonged with the leaves of *A. osmonti*. This, indeed, becomes the more probable with the observation that leaves

¹ Chaney, Carnegie Inst. Wash. Pub. No. 346, 126, pl. 18, figs. 7-9, 1927.

² Berry, U. S. Geol. Surv., Prof. Pap. 154-H, 255, pl. 57, fig. 2; pl. 63, fig. 11, 1929.

³ MacGinitie, *op. cit.*, No. 416, 62, pl. 11, figs. 2, 3, 1933.

⁴ Berry, U. S. Geol. Surv., Prof. Pap. 154-H, 255, pl. 57, fig. 2; pl. 63, fig. 11, 1929.

⁵ Knowlton, U. S. Geol. Surv., Bull. 204, 76, pl. 14, figs. 2, 3, 1902.

⁶ Berry, *op. cit.*, 255.

⁷ Chaney, Carnegie Inst. Wash. Pub. No. 346, 126, pl. 17, fig. 6; pl. 18, figs. 1, 3, 5, 7-9, 1927.

⁸ Chaney, *op. cit.*, pages 127, 128.

of the *A. negundo* type are missing, a situation which is duplicated in the Trout Creek flora.¹

Occurrence—Hog Creek, Locality 635; Cove Creek, Locality 637.

Collection—U. C. Mus. Palæobot., Nos. 1228, 1229.

Acer septilobatum Oliver

(Plate 3, fig. 5)

Acer septilobatum Oliver, Carnegie Inst. Wash. Pub. No. 455, 25, pl. 4, figs. 1, 2, 1934.

Acer cf. circinatum Chaney, Carnegie Inst. Wash. Pub. No. 349, 30, 1925.

The Weiser collections contain three incomplete leaves which are five or seven lobed, with coarse, pointed teeth and shallow, narrow sinuses. The preserved characters are essentially like those of *Acer septilobatum* Oliver from the Austin-Tipton flora. As pointed out in the original description, the leaves resemble most closely those of the living *A. circinatum* Pursh.

There is also in the collections a single maple fruit which is distinctive from the other fruits encountered, and which is essentially identical with fruits of *A. circinatum* studied in the writer's herbarium. In view of the presence of associated remains of both leaves and fruits of the *A. circinatum* type, the writer feels justified in referring the fruits also to the closely related fossil species, *A. septilobatum*. As fruits of this type have not previously been reported in the fossil state, it is thought best to include a brief description of the Weiser specimen.

Description—Fruit a broad, winged samara, 3 cm. long, and 1 cm. wide at the maximum width just above the middle; seed nucleus subcircular, 0.75 cm. in diameter; basal truncation straight and perpendicular to the long axis of the samara; wing thinly textured, clearly marked by fine veins.

Occurrence—Hog Creek, Locality 635; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1230.

Genus *TRAPA* Linné

Trapa prenata n. sp.

(Plate 3, fig. 6)

Four well-preserved and nearly complete fruits of this species were found at Locality 636. Their details are almost identical with those of the modern *Trapa natans* Linné., which were examined at The New York Botanical Garden.

Description—Fruits triangular, 2 to 3 cm. long, 3 to 4.5 cm. wide, evidently four-horned; the two horns shown in the plane of the impression long, thin and acuminate pointed, and projecting outward and slightly upward at, or nearly at, right angles to the short base of attachment; the remaining two horns represented merely by prominences or depressions in the upper central portion of the fruit; central body may or may not be marked by a pair of small rounded depressions near the lateral edge; base of attachment short and marked by striations which continue downward into the body of the fruit.

This species is evidently closely related to *Trapa americana* Knowlton from the Payette² and Esmeralda floras,³ differing chiefly in size and general shape, and in possessing four rather than two horns.

¹ MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 62, 1933.

² Knowlton, U. S. Geol. Surv., Eighteenth Ann. Rept., pt. 3, 733, pl. 102, fig. 7-a, 1898.

³ Berry, Proc. U. S. Nat. Mus., vol. 72, Art. 23, 13, pl. 2, figs. 5, 6, 1927.

In the closely related modern *T. natans*, the lateral horns usually project from the central instead of the upper part of the fruit. In other respects, it is essentially identical to the Weiser species. *T. natans* is at present not native to North America, but grows well under cultivation in the north-eastern states in ponds or slow streams.

Occurrence—North-South Highway, Locality 636.

Collection—U. C. Mus. Palæobot., Holotype No. 1231.

Genus ARBUTUS Linné

Arbutus matthesii Chaney

(Plate 3, fig. 9)

Arbutus matthesii Chaney, Carnegie Inst. Wash. Pub. No. 346, 131, pl. 20, figs. 1, 3-5, 1927.

Arbutus traini MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 64, pl. 12, fig. 3; pl. 13, figs. 1, 2, 1933.

Arbutus sp. Chaney, Carnegie Inst. Wash. Pub. No. 349, 36, 1925.

This species is represented in the Weiser collection by seven well-preserved specimens, several of which are virtually complete. These agree perfectly in all essential details with the specimens of *Arbutus traini* figured by MacGinitie from the Trout Creek flora. In his paper on the Upper Cedarville flora, LaMotte¹ has recently presented evidence for the inclusion of this species in *A. matthesii*.

At The New York Botanical Garden comparisons were made with all available species of *Arbutus* as well as with *Heteromeles* (*Photinia*) *arbutifolia* Roem., to which there is a marked resemblance. The Weiser forms resemble closely the lanceolate leaves which often occur as variants of the normal ovate leaves of the western *Arbutus menziesii* Pursh. In the character of veins, marginal teeth, cuneate base, and shape, they also bear a resemblance to the Mexican species *Arbutus varians* (= *mollis*) of Sheet No. 6813 and *A. varians* (= *laurina*) of Sheet No. 2995. In the large number and decurrency of the secondary veins, the specimens are clearly referable to *Arbutus* rather than *Heteromeles*.

In addition to the occurrences listed or mentioned above, *Arbutus matthesii* is also found in the Sucker Creek Miocene,² and the Payette specimen which Knowlton doubtfully referred to *Myrica* (?) *idahoensis*³ is essentially of the same type.

Occurrence—Hog Creek, Locality 635.

Collection—U. C. Mus. Palæobot., Plesiotype No. 1232.

Genus FRAXINUS (Tournefort) Linné

Fraxinus coulteri n. sp.

(Plate 3, figs. 3, 4)

Specimens of fruits which are so clearly referable to the genus *Fraxinus* and so well preserved as to make possible a complete description are abundant in the Weiser collections.

Description—Samaras oblong-lanceolate, $2\frac{1}{4}$ to $3\frac{3}{4}$ cm. long, including the wing; average length $2\frac{1}{4}$ cm.; seed body narrow-lanceolate, 1 to $1\frac{1}{2}$ cm. long, pointed at the base and rounded at the apex, wing 3 to 5 mm. wide,

¹ LaMotte, Carnegie Inst. Wash. Pub. No. 455, 1936.

² Brooks, Annals Carnegie Mus., vol. 24, 300, pl. 21, fig. 3, 1935.

³ Knowlton, U. S. Geol. Surv., Eighteenth Ann. Rept., pt. 3, 724, pl. 99, fig. 7, 1898.

clavate, widening gradually upward from the sides of the seed bodies and terminating in an abruptly rounded or slightly emarginate apex; wing clearly marked by numerous, fine longitudinal veins, of which the central one is the most prominent.

Among modern species which were compared at The New York Botanical Garden, the fruits of *Fraxinus oregona* Nutt. are virtually identical. The range of variations in size and shape were noted in many clusters of fruits from a single tree, and every specimen in the Weiser collections could be matched perfectly with a modern counterpart.

It is remarkable that leaves referable to *Fraxinus* are extremely rare in the Weiser collections. Such incomplete specimens as were found, however, bear a striking resemblance to the entire-margined leaves of the modern *Fraxinus oregona*. The scarcity of leaves of species which ordinarily grow along stream and lake banks can in large part be accounted for by the somewhat xeric conditions indicated by the flora as a whole, as pointed out on page 119.

Well-preserved fruits of *Fraxinus* are apparently rare in the Tertiary deposits of the West. MacGinitie records but does not figure "characteristic seeds of *Fraxinus*, together with fragmentary leaves" from the Trout Creek Miocene, and mentions a similar species collected by Chaney from the Mascall;¹ LaMotte figures a poorly preserved seed from the Upper Cedarville formation which he related to the modern *F. oregona*.² These may belong to the new species described. The Pliocene species *F. caudata* Dorf,³ which is not represented by fruits, apparently had a more lanceolate leaf than the Weiser species. The specimens from the Latah, questionably called samaras of *Fraxinus*,⁴ are too poorly preserved to make a comparison possible. The small fruits of *F. idahoensis* Brown from the Latah of Idaho⁵ are of a distinctly different type.

The species is named in honor of Mr. John H. Coulter, Princeton, '30, who rendered valuable field assistance in Idaho.

Occurrence—Hog Creek, Locality 635; North-South Highway, Locality 636; Alkali Creek, Locality 638.

Collection—U. C. Mus. Palæobot., Cotypes Nos. 1233, 1234.

INCERTÆ SEDIS

Cf. *Quercus horniana* Lesquereux

Quercus horniana Lesquereux, Proc. U. S. Nat. Mus., vol. 11, 17, 1888.

Quercus horniana Lesquereux, U. S. Geol. Surv., Bull. 204, 52, pl. 8, fig. 1, 1902.

A single specimen of the lower half of a leaf is identical with the figured specimen of cf. *Quercus horniana* from the Austin-Tipton flora.⁶ Both Knowlton and Miss Oliver have expressed doubt as to the generic reference. It is possible that it may be a species of *Fagus* or *Castanea*. Unfortunately the Weiser material is inadequate for making a more complete determination.

Occurrence—Cove Creek, Locality 637.

Collection—U. C. Mus. Palæobot., No. 1235.

¹ MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 66, 1933.

² LaMotte, Carnegie Inst. Wash. Pub. No. 455, 1936.

³ Dorf, Carnegie Inst. Wash. Pub. No. 412, 106, pl. 13, figs. 6, 7, 8, 1930.

⁴ Berry, U. S. Geol. Surv., Prof. Pap. 185-E, 122, pl. 24, figs. 3, 4, 1934.

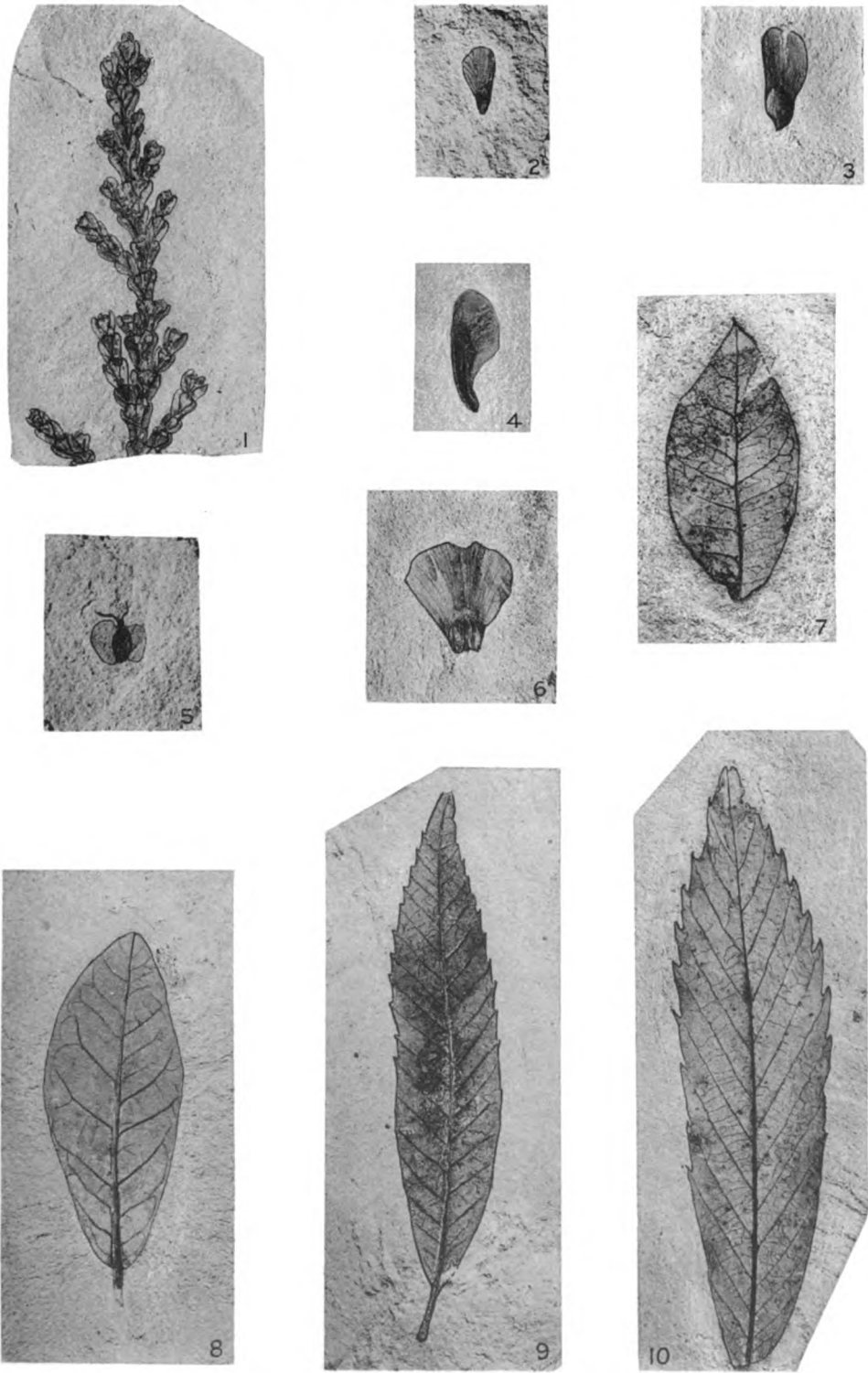
⁵ Brown, Jour. Paleont. vol. 9, No. 7, 583, pl. 67, fig. 14, 1935.

⁶ Oliver, Carnegie Inst. Wash. Pub. No. 455, 27, pl. 5, fig. 5, 1934.

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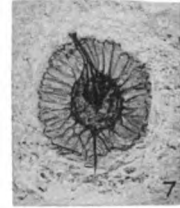
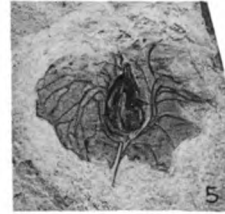
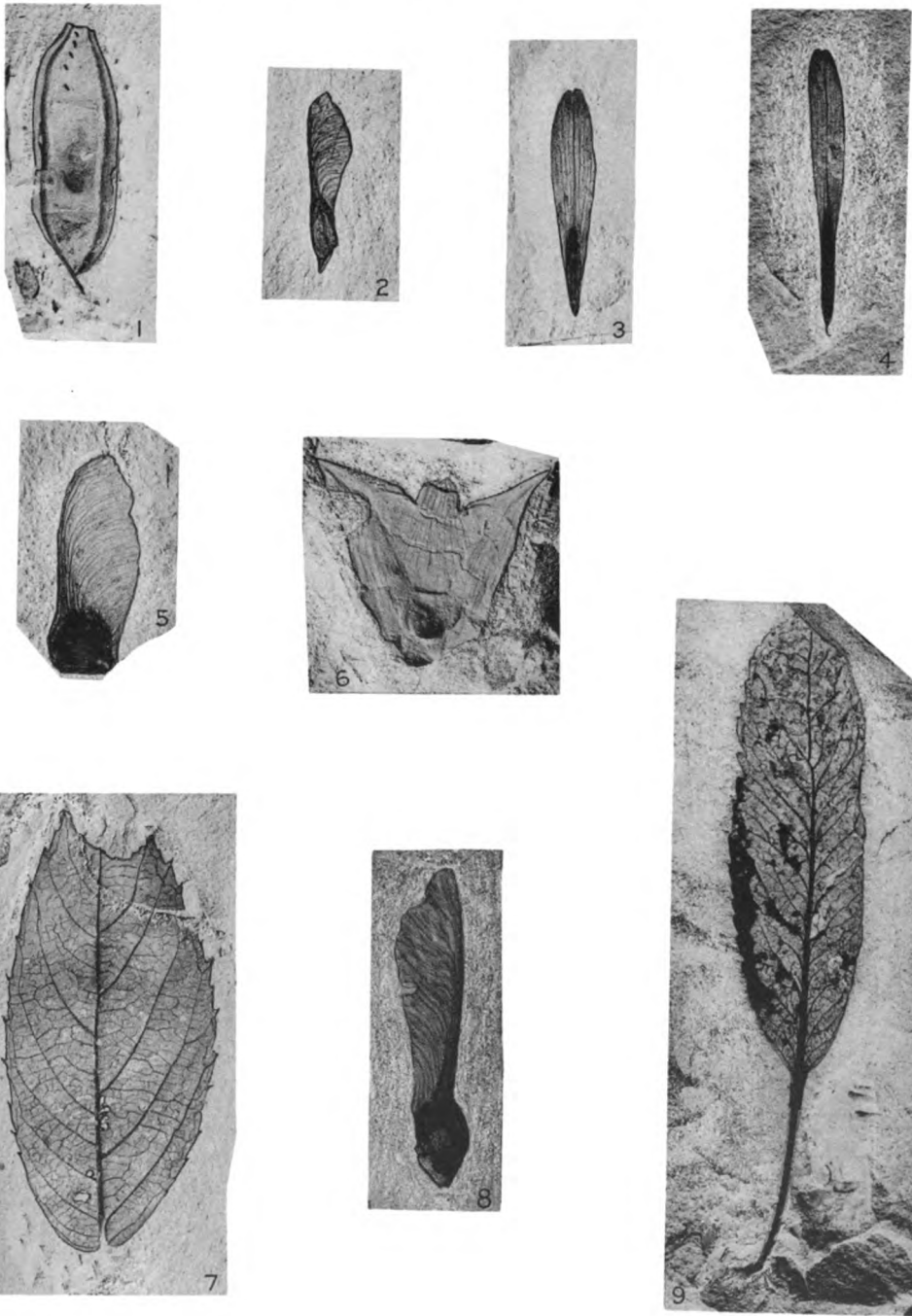


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CONTRIBUTIONS TO PALÆONTOLOGY

III

**A PLIOCENE FLORA FROM THE MOUNT EDEN BEDS,
SOUTHERN CALIFORNIA**

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With six plates and one text-figure

[Issued May 28, 1937.]

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A PLIOCENE FLORA FROM THE MOUNT EDEN BEDS, SOUTHERN CALIFORNIA

INTRODUCTION

The palæobotanical record is incompletely known in one of its most critical phases, the Pliocene; floras of this epoch are comparatively rare and most of them are represented by few species. Upon the record of their occurrence depends in large measure the interpretation of modern vegetation. This is especially true in western North America, where, at the close of the Tertiary and in the Quaternary, geologic and climatic changes resulted in major biotic disturbances. Since the flora of the Mount Eden beds near Beaumont, California, is relatively large and is located near the border of three botanical provinces—the California, Great Basin, and Sonoran—it is in a strategic position to afford evidence relative to the origin and migration of certain California forests. In none of the fossil deposits previously studied in western America has there been found an adequate record of the digger pine (*Pinus sabiniana* Dougl.) forest¹ now characteristic of the foothills of the Great Valley of California, nor of the big-cone spruce (*Pseudotsuga macrocarpa* Mayr.) forests of southern California.² The Mount Eden flora contains representatives of these forests, in addition to a Sonoran element and abundant chaparral remains.

Concretions containing plant remains were first recorded from the Mount Eden beds by Fraser;³ subsequently, Mr. Guy Hazen collected plant material from that area for the American Museum of Natural History. A preliminary list of 12 species of plants, all referable to Pliocene species described by Dorf,⁴ was recognized by Chaney from this collection.⁵ A

¹ Dorf, Carnegie Inst. Wash. Pub. No. 412, 1930, recorded a cone in the Pico sandstones of Lower Pliocene age. Chaney and Mason, Carnegie Inst. Wash. Pub. No. 415, 1930, found a well-worn cone scale in the Pleistocene deposits at Carpinteria.

² As used in this report, the term southern California includes the nine southern counties of the state, and is defined by the area lying south of the Santa Ynez Mountains, the Mount Pinos region, and the Tehachapi Mountains. It is bounded on the east by the Mohave and Colorado Deserts, and on the west by the Pacific Ocean; southward, the flora passes gradually into Baja California and northern Mexico. The flora of southern California is distinct in its chaparral climax and is characterized by many endemics. A number of species range northward into the Coast Ranges or the lower southern Sierra Nevada Mountains, but find their greatest development and characteristic expression in southern California.

Southern California may be considered to consist of two parts: (a) The San Gabriel, San Bernardino, and San Jacinto Valleys form a definite inland area. They are bounded on the east by the respective mountain ranges for which they are named, and on the west by the Puente Hills and Santa Ana Mountains. Southward, the interior region is terminated by the cross-ranges near Palomar Mountain, and northward it extends 125 miles to the San Fernando Valley. (b) Bordering the west flanks of the Puente Hills and the Santa Ana Mountains, and extending to the ocean, is a true coastal area which is continually exposed to more humid conditions. Although these two areas are floristically distinct, there is an intermingling of species between them.

³ State Calif. Div. Mines, vol. 27, no. 4, 513, 1931.

⁴ *Op. cit.*

⁵ See Frick, Bull. Amer. Mus. Nat. Hist., vol. 59, art. 9, 517, 1933.

field party from the Los Angeles Museum also collected plant remains at various localities in the Mount Eden beds. In 1934 the writer studied representative loan collections from the American Museum of Natural History and the Los Angeles Museum, as well as additional material from Mr. Hazen's collection, on the basis of which a preliminary report was published by the American Museum of Natural History.¹ Grateful acknowledgment is made to Messrs. W. A. Bryan, Director of the Los Angeles Museum, Childs Frick of the American Museum of Natural History, and Guy Hazen, for their cooperation in making their collections available for study.

The investigation of the Mount Eden flora was undertaken at the suggestion of Professor Ralph W. Chaney of the University of California, whose continued interest and encouragement are gratefully acknowledged. Thanks are also given to Dr. H. L. Mason, who has offered many valuable suggestions; to Mr. A. E. Wieslander, of the California Forest and Range Experiment Station, Berkeley, for the use of vegetation type maps of southern California; to the Carnegie Institution of Washington, which supplied the necessary funds for field work; and to Mr. Frick for assistance in the purchase of important type specimens.

From the winter to summer of 1935, and again in the summer of 1936, the writer was engaged in field work throughout southern California, and was afforded an excellent opportunity to make a detailed study of the living vegetation. This survey of the present vegetation in southern California has served as a basis for the interpretation of the Mount Eden flora.

GEOLOGIC RELATIONS

The Mount Eden formation is well exposed south of Beaumont, which is located on the western end of the San Geronio Pass between the San Bernardino and San Jacinto Mountains of southern California. These beds have been recognized by Fraser² as being composed of two phases: a lower red-bed member, in which no fossils have been found; and the upper Mount Eden member, which contains both vertebrate and plant remains.

Red-bed member. The lower conglomeratic red-beds grade upward into gray, gritty sandstones. In the upper part gray-green grits and sandstones predominate and they are better sorted and stratified than the basal red-beds. The lower strata apparently represent a conglomerate deposited by streams flowing from adjacent highlands of igneous and metamorphic material, while the upper strata were evidently deposited in a shallow lake basin. This member strikes northwest and dips to the northeast at angles ranging from 9° to 18°, and is approximately 1800 feet thick.

Mount Eden member. The Mount Eden member, which conformably overlies the red-beds, extends over an area of about 10 square miles and has an estimated thickness of 1500 feet; the attitude of this member is similar to that of the red-beds. The Mount Eden member is composed of

¹ Amer. Mus. Novitates, No. 729, 1934.

² For a complete discussion of the geology of this area see: Fraser, State Calif. Div. Mines, vol. 27, no. 4, 1931; Frick, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 12, no. 5, 1921.

poorly indurated shales and sandstones. Gritty interbeds are common and the sands are cross-bedded and exhibit rapid lateral gradation to finer sands and silts; ripple marks occur throughout. The micaceous, calcareous sandstones are gray to brownish colored and are more abundant to the west, while eastward, beyond Lamb Canyon, buffy lenticular shales are common.

The Mount Eden flora is found scattered along outcrops through the middle portion of this member. The plant-bearing strata are difficult to follow for any considerable distance, as all exposures are on steep south slopes where slumping is common. Leaves occur as impressions in the finer sandstones, while cones, cone scales, and seeds are represented by petrified material. Concretions containing plant material, as well as cones and seeds, were collected following exposure by weathering.

Concerning the later geologic history of the area, Mendenhall¹ states that "Sometime after the deposition of the . . . clays, a crustal movement began which . . . seems to have elevated the San Bernardino Mountains . . . until . . . they were [somewhat] lower than at present. . . . Mountain streams carried the products of their erosional activity out onto the lowlands . . . until many hundreds of feet were piled up. [San Timoteo.]"

San Timoteo formation. Several fragmental casts of cone scales were found in this formation, which is of Upper Pliocene age. These deposits form the Badlands to the west of Beaumont and unconformably overlie the Mount Eden formation. The San Timoteo beds are characterized by coarse yellowish sands and cobble beds which are cross-bedded and exhibit rapid lateral variation and channeling; interbeds of finer gray-brown sands and clays occur throughout. This formation is evidently a fanglomerate deposited in a semiarid region.

Active vertical movement commenced during the Quaternary along the numerous faults throughout southern California. Vaughn² demonstrates that ". . . the San Bernardino Mountains owe their existence to a great system of Quaternary faults. . . . The uplift was not continuous, but by progressive stages. . . . The mountains reached a great height [10,000 to 11,000 feet in the southern part of the range] . . . and . . . glaciers were developed along the north side of the highest ridge, but were of short duration." The elevation of the San Jacinto Mountains has been almost continuous since the deposition of the red-beds.³

Briefly summarizing, the Mount Eden formation is composed of a lower conglomeratic red-bed member and an upper Mount Eden member of sandstones and shales. These upper strata contain both plant and vertebrate remains, and were apparently deposited in an arid climate. The San Timoteo beds, which unconformably overlie the Mount Eden formation, represent a fanglomerate of an arid region; fragments of cone scales have been collected in this formation. The period of major uplift of the mountains adjacent to the Beaumont area was during the Quaternary.

¹ U. S. Geol. Surv. Water Supply and Irrigation Paper 142, 30, 1905.

² Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 13, no. 9, 405, 1922.

³ Fraser, State Calif. Div. Mines, vol. 27, no. 4, 504, 537, 1931.

COMPOSITION OF THE FLORA

The Mount Eden flora contains 30 species, representing 21 genera and 16 families. Twenty-two of the species are dicotyledons, of which 7 are arborescent, 3 are normally small trees, and 12 definitely shrubby. Of the remainder 6 are conifers, and the monocotyledons and pteridophytes are both represented by single species. Nine species of the Mount Eden flora have been previously recorded from other Pliocene floras, and the others are described as new. As far as known, *Prosopis* and *Lepidospartum* are genera new to the fossil record.

SYSTEMATIC LIST OF SPECIES

Pteridophyta	Dicotyledonæ— <i>continued</i>
Equisetales	Rosales
Equisetaceæ	Platanaceæ
Equisetum sp.	Platanus paucidentata
Spermatophyta	Rosaceæ
Gymnospermæ	Cercocarpus cuneatus
Coniferales	Prunus preandersonii
Pinaceæ	Prunus prefremontii
Pinus hazeni	Leguminosæ
Pinus pieperi	Prosopis pliocenica
Pinus pretuberculata	Sapindales
Pseudotsuga premacrocarpa	Anacardiaceæ
Cupressaceæ	Rhus prelaurina
Cupressus preforbesii	Sapindaceæ
Gnetales	Sapindus lamottei
Gnetaceæ	Rhamnales
Ephedra sp.	Rhamnaceæ
Angiospermæ	Ceanothus edensis
Monocotyledonæ	Ceanothus sp.
Pandanales	Ericales
Typhaceæ	Ericaceæ
Typha lesquereuxii	Arbutus sp.
Dicotyledonæ	Arctostaphylos preglaucæ
Salicales	Arctostaphylos prepungens
Salicaceæ	Gentianales
Populus pliotremuloides	Oleaceæ
Salix coalingensis	Fraxinus edensis
Salix sp.	Asterales
Juglandales	Compositæ
Juglandaceæ	Lepidospartum sp.
Juglans beaumontii	
Fagales	
Fagaceæ	
Quercus hannibali	
Quercus lakevillensis	
Quercus orindensis	
Quercus pliopalmeri	

A number of the species are of infrequent occurrence, and of these *Arbutus* sp., *Lepidospartum* sp., *Rhus prelaurina*, and *Salix* sp. are represented by single impressions. Except for *Rhus*, which has been previously recorded,¹ they were not named because of their inadequate representation. *Sapindus lamottei* was determined from an individual but complete, well-preserved seed, and *Ephedra* sp. from a carbonized stem.

As the plant remains are scarce, only a general statement can be offered as to their relative dominance in the flora. The following list gives the approximate order of abundance of the trees:

Platanus paucidentata (leaves)
Pseudotsuga premacrocarpa (cones)
Pinus pieperi (cones, seeds, scales)
Pinus hazeni (cones, seeds, scales)
Juglans beaumontii (fruits and a leaflet)
Salix coalingensis (leaves)
Populus plotremuloides (leaves)
Pinus pretuberculata (cones)

Each of the other trees is represented by several leaves, or by two cones in the case of *Cupressus*. Of the shrubs, *Quercus pliopalmeri* (leaves) and *Prunus prefremonitii* (seeds) are the most abundant, while several specimens characterize each of the other species. Impressions of *Typha* are common at most localities.

The composition of the Mount Eden flora is unique among the later Tertiary assemblages, since it contains species representing three distinct plant associations of which this constitutes the first extensive fossil record. The flora includes an extreme xeric association, which is recognized as a desert-border unit, a coniferous element directly related to living endemic conifers in California, and abundant chaparral remains. These associations will be considered in detail in the discussion of the habitat relations of the flora.

PHYSICAL CONDITIONS

Evidence as to the environmental conditions existing in the Mount Eden area in the Pliocene will be derived from a consideration of the geologic relations, the fossil plants, and the associated vertebrates. As the geologic relations and the associated mammals afford critical evidence relative to the interpretation of the Mount Eden flora, they will be considered first. In determining the habitat conditions and the topographic setting of the flora, a detailed comparison of living vegetation similar to the fossil flora will be presented.

¹ Fragments of a *Rhus* in the Orinda flora were referred to *R. laurina*. See Dorf, Carnegie Inst. Wash. Pub. No. 412, 100, 1930.

CONDITIONS SUGGESTED BY THE GEOLOGIC RELATIONS

In addition to considering the topography and the physical conditions which obtained in the Mount Eden area in the Pliocene,¹ the subsequent geologic and climatic changes must also be determined, for they are directly involved in the interpretation of the floral change in the Beaumont area since Mount Eden time. The following points afford evidence relative to the environmental conditions existing in the Beaumont area during and following the Mount Eden epoch.

1. The character of the sediments is indicative of an arid climate in the basin of deposition.²

2. The existence of numerous shallow lakes and playas in the present Colorado and Mohave Deserts during the Pliocene and Pleistocene is evidenced by wide-spread deposits.³ That such lakes would have had a moderating influence on the Mount Eden area in the Pliocene is somewhat doubtful,⁴ though they probably afforded conditions requisite for the existence of riparian and aquatic-border species in those areas.

3. Both Clark⁵ and Reed⁶ have demonstrated that the present southern California coastline was submerged in the Pliocene, and that the marine incursion existed into the Pleistocene. This embayment may have exerted a moderating influence on the Mount Eden area, for the Santa Ana Mountains and Puente Hills, which form the present western boundary of interior southern California, were somewhat lower at this time.⁷ However, the abundant development of xeric associations in the flora suggests that the moderating effects of this Pliocene sea were not great.

4. The Mount Eden area is now approximately 2500 feet in elevation; Mendenhall⁸ has shown that it was nearer sea-level in the Pliocene period.

5. Since the San Bernardino and San Jacinto Mountains were much lower during the Mount Eden epoch than at present,⁹ and the Santa Ana Mountains and Puente Hills were likewise of less elevation at this time, interior southern California was not as narrowly restricted a biogeographical unit as at present.

With the retreat of the marine embayment, and the elevation of the mountains to the east and west, interior southern California was definitely delimited. The present high temperatures and low humidity in this interior

¹ Since the flora is probably of late Middle Pliocene age, the general implications are in direct relation to this portion of the period, and the following events.

² Frick, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 12, no. 5, 285, 338, 1921; Fraser, State Calif. Div. Mines, vol. 27, no. 4, 512, 1931.

³ Brown, U. S. Geol. Surv. Water Supply and Irrigation Paper 497, 44-47, 1923; Reed, *Geology of California*, 257, 1933.

⁴ Professor John Leighly, oral communication, March 9, 1936.

⁵ Jour. Geol., vol. 29, 612, 1921.

⁶ *Op. cit.*, 252, 1933.

⁷ English, U. S. Geol. Surv. Bull. 768, 48, 1926; Dickerson, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 8, no. 11, 270, 1914.

⁸ U. S. Geol. Surv. Water Supply and Irrigation Paper 142, 30, 1905.

⁹ Vaughn, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 13, no. 9, 405, 1922; Fraser, State Calif. Div. Mines, vol. 27, no. 4, 537, 1931.

area are partly the result of these late Tertiary and Quaternary geologic changes.

Aside from these palæogeographic and climatologic considerations, the Mount Eden sediments and the occurrence of plant remains in them also afford evidence relative to the nature of the habitat and the climate in the Mount Eden basin. Exposed playa deposits of the Mount Eden beds, now to be seen on hilltops in the Mount Eden area, are indicative of shallow lakes existing in the Mount Eden basin. The abundance of ripple marks, as well as the cross-bedding and rapid lateral gradation of the sediments, is further corroborative of shallow water conditions. A petrographic analysis of the Mount Eden sediments¹ indicates that they were deposited under arid conditions. In addition to this evidence from the character of the sediments, the manner of preservation of the leaves, which are typically curled and scattered throughout the sediments, is consistent with a subaerial site of deposition in an arid climate, in which the leaves would be curled from drying and scattered by the wind.

FAUNAL RELATIONSHIPS

The vertebrate remains associated with the fossil plants are of importance in indicating the nature of the Pliocene habitats in the Mount Eden area. The age of the deposits, as suggested by the vertebrate fauna, will be considered on a later page.

Abundant mammalian remains have been described by Frick² from the Mount Eden formation in the area to the west of the plant localities. More recently, vertebrate remains have been found in association with the flora and include the following:³

Rodentia	Perissodactyla
Hypolagus	Equidæ
Carnivora	Pliohippus edensis
Procyonine sp.	Pliohippus osborni
? Plesioguline sp.	Rhinocerotidæ
Ursidæ	Teleocerine
Hyænarctos gregorii	Artiodactyla
Canidæ	Suidæ
Plionarctus edensis	Prosthennops edensis
Hyænognathine	Platygonus sp.
Felidæ (form)	Camelidæ
Edentata	Pliauchenia merriami
Nothrotherium? sp.	Prochenia edensis
Megalonyx? sp.	Cervidæ?
	Antilocapridæ
	Proboscidea
	Rynchotherium edensis

¹ Frick, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 12, no. 5, 338, 1921.

² *Op. cit.*

³ Frick, Bull. Amer. Mus. Nat. Hist., vol. 59, art. 9, 516, 1933.

Concerning the habitat conditions suggested by the vertebrate fauna from the Mount Eden beds proper, where many of the above listed species also occur, Frick¹ states: "It was an interesting assemblage that then roamed the Eden wilds. Grazing over the open stretches were . . . horses . . . camel . . . antelope, and . . . deer. Within the edge of the scrub might have been seen pigs and larger boar, or . . . occasional . . . four-toothed proboscideans. In the forests lived sabre-toothed cats . . . wolves, and huge bear."

The Pleistocene Bautista deposits, several miles southeast of the Mount Eden deposits, contain vertebrates indicative of forest and plains-grazing types, and constitute a new fauna in the region.

VERTEBRATES OF THE BAUTISTA BEDS²

Rodentia	Artiodactyla
Lepus sp.	Camelidæ
Edentata	Camelid? sp.
Megalonyx? sp.	Cervidæ
Perissodactyla	Odocoileus? sp.
Equidæ	Antilocapridæ
Equus bautistensis	Capromeryx? sp.
Tapiridæ	Antilocapra? sp.
Tapirus merriami	

The mammalian faunas of the Beaumont region afford the following critical evidence relative to the interpretation of the Mount Eden flora: (1) The Mount Eden fauna substantiates the presence of a low-lying basin with an adjacent plains-savanna habitat, and adjoining forested uplands. (2) The presence of vertebrates indicative of plains-grazing types in the Bautista beds suggests that conditions suited to such vegetation continued into the Pleistocene, and that the wide-spread development of the chaparral which dominates the area today occurred subsequently.

BOTANICAL FEATURES OF THE MOUNT EDEN FLORA

PRESENT DISTRIBUTION OF THE MODERN EQUIVALENTS OF THE FLORA

The succession of fossil floras since the early Tertiary gives evidence of widely changing physical conditions, species evolution and extinction, and climatic selection and segregation of elements or species of the floras. Since a great lapse of time involves changing floral composition, it is difficult in many cases to duplicate an older Tertiary flora among living forests, or to visualize the conditions under which it existed. The difficulties of applying an ecologic interpretation to these early Tertiary assemblages are to a great extent eliminated in a study of Pliocene floras. Through a survey of the modern plants represented by related equivalents in a late Tertiary flora, one may determine with reasonable accuracy the physical conditions which existed in the epoch. This is especially true where the fossil species are closely similar to their living equivalents, as in the Mount Eden flora.

¹ Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 12, no. 5, 285, 1921.

² *Ibid.*, 283-288, 1921.

With regard to the interpretation of the Mount Eden flora, the vegetation of two areas in southern California shows a definite relationship to the fossil assemblage; the significance of a third area lies in its coniferous association. These three localities may be designated as follows: (a) the Sierra Peak region in the northern Santa Ana Mountains, 35 miles west of the fossil area; (b) the desert slopes of the San Bernardino and San Jacinto Mountains, to the east of the Mount Eden area; and (c) the City Creek Road on the western slope of the San Bernardino Mountains, 15 miles northwest of the Mount Eden beds. To facilitate a comparison of the Mount Eden flora with the vegetation of these three areas, table 1 was prepared; the accompanying map (fig. 1) indicates the geographic areas referred to.

A study of the present flora on the north slope of Sierra Peak is particularly enlightening, since 63 per cent of the living equivalents of the fossil flora occur at this locality. It is significant that the most xeric association of the flora, the desert-border element, is not present in this area. The species representing this xeric unit, namely *Ephedra* sp., *Prosopis juliflora* var. *glandulosa*, *Prunus andersonii*, *Prunus fremontii*, and *Quercus palmeri*, may be found on the desert slopes of the San Bernardino and San Jacinto Mountains. It is to be noted that the species common to the Sierra Peak area and to the desert region are typically riparian (*Platanus*, *Salix*, *Lepidospartum*), or are chaparral species (*Ceanothus*, *Cercocarpus*, *Arctostaphylos*), or are confined to favorable, cool north slopes and canyons several miles from the edge of the desert (*Pinus*, *Pseudotsuga*, *Quercus*).

Of particular interest on the City Creek Road is the association of *Pinus coulteri*, *Pinus tuberculata*, and *Pseudotsuga macrocarpa*, as illustrated in Plate 1, figure 2. The relative abundance of the fossil equivalents of these species in the Mount Eden flora suggests a similar coniferous association on the slopes bordering the Mount Eden basin. Many of the associates of these conifers in this area are also represented in the Mount Eden flora by equivalent species.

Of the plants with a distribution outside of southern California, *Pinus sabiniana* and *Quercus douglasii* are living equivalents of Mount Eden species representing the digger pine forest, which is well developed in the foothills surrounding the Great Valley of California. The most southern occurrence of this forest is at Antelope Valley, 100 miles north of the Mount Eden area. *Sapindus drummondii* and *Arbutus zalapensis* are living representatives of Mount Eden species which constitute a Sonoran element in the flora no longer found in California.

Thus, from a distributional standpoint, the modern equivalents of the Mount Eden flora may be considered to consist of several units: (a) an assemblage on the north slope of Sierra Peak, 35 miles west of Beaumont, constituting 63 per cent of the flora; (b) a desert-border element on the edge of the Colorado Desert, some 15 miles east of the fossil area; (c) a digger pine forest 100 miles to the north, and (d) a Sonoran element now existing in the Southwest and northern Mexico.

TABLE 1—*Distribution of the modern equivalents of the fossil species*

Fossil species	Modern equivalent	Southern California				Nearest locality
		Sierra Peak	City Creek Road	Desert slopes *		
<i>Arbutus</i> sp.	<i>Arbutus xalapensis</i> H. B. K.	X				Mexican plateau
<i>Arctostaphylos preglaucia</i>	<i>Arctostaphylos glauca</i> Lindl.		X		X	
<i>Arctostaphylos prepungens</i>	<i>Arctostaphylos pungens</i> H. B. K.				X	
<i>Ceanothus</i> sp.	<i>Ceanothus cuneatus</i> Nutt.	X	X			
<i>Ceanothus edensis</i>	<i>Ceanothus divaricatus</i> Nutt.	X	X		X	
<i>Cercocarpus cuneatus</i>	<i>Cercocarpus betuloides</i> Nutt.	X			X	Antelope Valley
<i>Cupressus preforbesii</i>	<i>Cupressus forbesii</i> Jepson	X				
<i>Ephedra</i> sp.	<i>Ephedra</i> spp.				X	
<i>Equisetum</i> sp.	<i>Equisetum</i> spp.	X				
<i>Fraxinus edensis</i>	<i>Fraxinus dipetala</i> H. & A.	X	X			
<i>Juglans beaumontii</i>	<i>Juglans californica</i> Wats.	X			X	Antelope Valley
<i>Lepidospartum</i> sp.	<i>Lepidospartum squamatum</i> Gray	X	X			
<i>Pinus hazeni</i>	<i>Pinus coulteri</i> Don.	X	X		X	
<i>Pinus pieperi</i>	<i>Pinus sabiniana</i> Dougl.					
<i>Pinus pretuberculata</i>	<i>Pinus tuberculata</i> Gord.	X	X			
<i>Platanus paucidentata</i>	<i>Platanus racemosa</i> Nutt.	X			X	San Bernardino Mts.
<i>Populus pliotremuloides</i>	<i>Populus tremuloides</i> Michaux.					
<i>Prosopis pliconica</i>	<i>Prosopis juliflora</i> DC. var <i>glandulosa</i> Ckll.					
<i>Prunus preandersonii</i>	<i>Prunus andersonii</i> Gray				X	
<i>Prunus prefremontii</i>	<i>Prunus fremontii</i> Wats.				X	
<i>Pseudotsuga premacrocampa</i>	<i>Pseudotsuga macrocarpa</i> Mayr.		X		X	Antelope Valley
<i>Quercus lakevillensis</i>	<i>Quercus agrifolia</i> Née.	X				
<i>Quercus hamnibali</i>	<i>Quercus chrysolepis</i> Liebm.	X	X		X	
<i>Quercus orindensis</i>	<i>Quercus douglasii</i> H. & A.					
<i>Quercus piopalmeri</i>	<i>Quercus palmeri</i> Engelm.					
<i>Rhus prelaurina</i>	<i>Rhus laurina</i> Nutt.	X			X	Arizona
<i>Salix coalingensis</i>	<i>Salix lasiolepis</i> Benth.	X	X		X	
<i>Salix</i> sp.	<i>Salix exigua</i> Nutt.	X	X		X	
<i>Sapindus lamottei</i>	<i>Sapindus drummondii</i> H. & A.					
<i>Typha lesquereuxi</i>	<i>Typha angustifolia</i> L.	X				
Total.....		19	13	16		
Percentage.....		63	43	53		

* Desert slopes of the San Bernardino and San Jacinto Mountains.

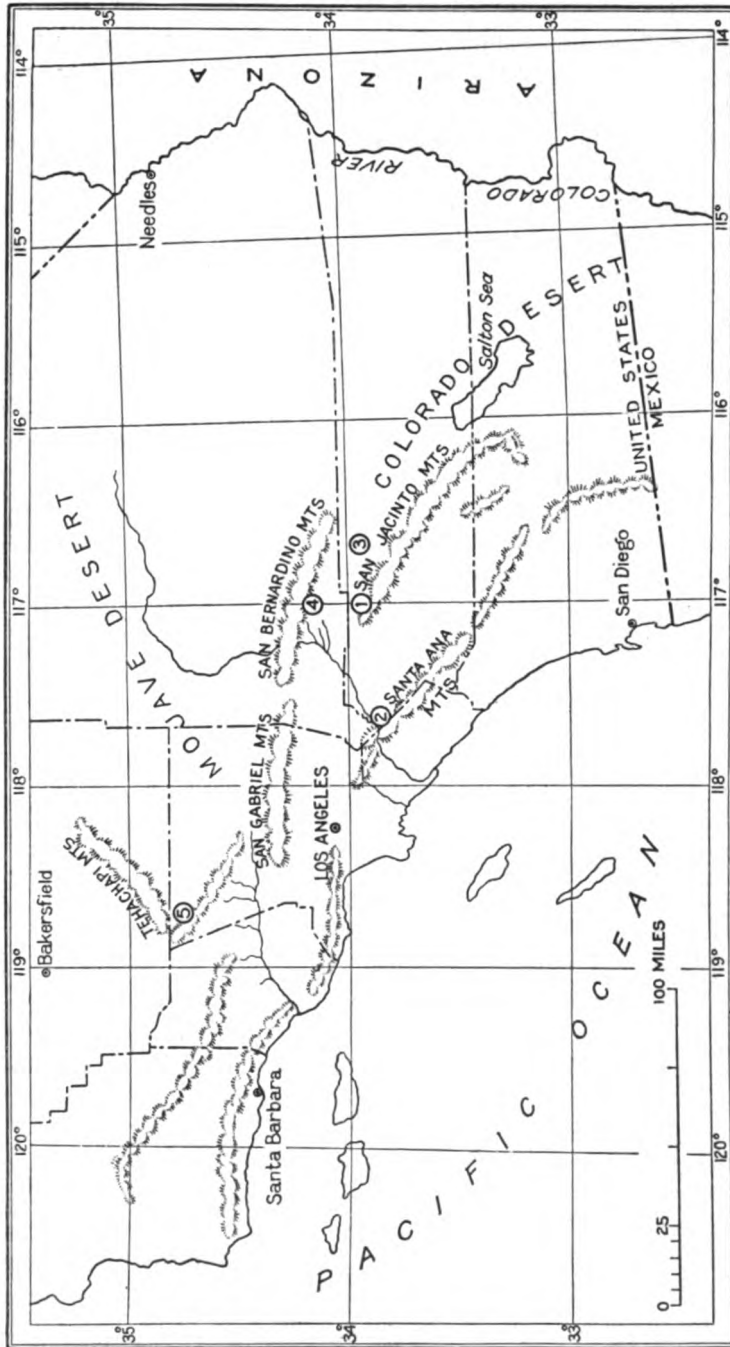


FIG. 1—Sketch map of southern California

- 1. Fossil locality
- 2. Sierra Peak area
- 3. Desert slopes
- 4. City Creek Road
- 5. Antelope Valley

PLANT ASSOCIATIONS REPRESENTED IN THE FLORA

In dividing any flora into habitat groups it is evident that transitional types or ecotones occur, resulting in mixed or mosaic plant associations between the definite habitats. Such vegetative types are common in southern California, and, in fact, in all areas where rapid topographic changes accompanied by an increase or decrease in humidity or temperature produce marked floral associations. On the mountain slopes in the Sierra Peak and City Creek areas, and on the east slopes of the San Bernardino and San Jacinto Mountains, climate and vegetation vary progressively with altitude. As a direct result of slope exposure, species may occur lower down on north and higher up on south slopes. Along streams and on flood-plains plants may be carried below their normal lower ecologic borders. It is significant that the Mount Eden flora suggests a topographic control of vegetation, resulting in diversified types within limited areas, similar in aspect to that now extant in southern California.

A survey of the living equivalents of the Mount Eden flora indicates that the fossil assemblage may be grouped into six habitat associations, as listed below. Since the fossil species closely resemble their modern representatives, it is believed that the habitat implications of the fossil and living species are quite similar. Hence, in the following discussion of the ecologic relations, a direct reference is made to the modern equivalents of the fossil flora.

MOUNT EDEN SPECIES LISTED BY ASSOCIATIONS

Desert-border element

- Ephedra sp.
- *Lepidospartum sp.
- Prosopis pliocenica
- Prunus preandersonii
- Prunus prefremontii
- *Quercus pliopalmeri
- *Sapindus lamottei

Lake-border or marsh†

- Equisetum sp.
- Typha lesquereuxi

Riparian

- *Fraxinus edensis
- *Juglans beaumontii
- *Lepidospartum sp.
- Platanus paucidentata
- Populus pliotremuloides
- Salix coalingensis
- Salix sp.
- *Sapindus lamottei

Savanna and woodland

- Arbutus sp.
- *Juglans beaumontii
- Pinus pieperi
- Quercus hannibali
- Quercus lakevillensis
- Quercus orindensis

Chaparral

- Arctostaphylos preglaucia
- Arctostaphylos prepungens
- Ceanothus edensis
- Ceanothus sp.
- Cercocarpus cuneatus

- *Fraxinus edensis
- *Quercus pliopalmeri
- Rhus prelaurina

Coniferous associations

- Cupressus preforbesii
- Pinus hazeni
- Pinus pretuberculata
- Pseudotsuga premacrocampa

* Species preceded by an asterisk may normally occur as a dominant in more than one habitat.

† Most of the riparian genera may also be present about the borders of lakes or marshes.

Desert-border Element

The desert-border unit is composed of species whose living representatives are characteristic of arid regions throughout their range, and all are found bordering desert areas. They may grow on desert slopes and along desert drainages, or may be present on deserts opposite the mouths of streams where moisture is more available than in the desert proper. True desert conditions such as are found in the present adjacent Colorado Desert may not have been existent in the basin during Mount Eden time, but certain species do indicate conditions which now occur along the borders of this desert. The ecologic occurrence of the living equivalents of this xeric association is presented below, following which the present distribution of this unit in the area to the east of the Mount Eden region will be considered.

FOSSIL SPECIES AND MODERN EQUIVALENTS OF THE DESERT-BORDER ELEMENT

Fossil species	Modern equivalents
<i>Ephedra</i> sp.	<i>Ephedra</i> spp.
<i>Lepidospartum</i> sp.	<i>Lepidospartum squamatum</i>
<i>Prosopis pliocenica</i>	<i>Prosopis juliflora</i> var. <i>glandulosa</i>
<i>Prunus preandersonii</i>	<i>Prunus andersonii</i>
<i>Prunus fremontii</i>	<i>Prunus fremontii</i>
<i>Quercus pliopalmieri</i>	<i>Quercus palmeri</i>
<i>Sapindus lamottei</i>	<i>Sapindus drummondii</i>

Ephedra is abundant on the Colorado and Mohave Deserts, and throughout the Southwest. On the deserts it has been noted in association with all of the other species of the desert-border element, and may grow with riparian species which approach desert areas.

Lepidospartum is typically found in desert washes and may be associated with the other species of this unit on the edge of the Colorado Desert. *Lepidospartum* also grows with digger pine, which is abundantly represented in the flora by its fossil equivalent *Pinus pieperi*, at the southern limit of the forest on the edge of the Mohave Desert. On flood-plains in interior southern California, *Lepidospartum* may be associated with several riparian species which have Mount Eden equivalents, namely, *Juglans californica*, *Platanus racemosa*, *Salix exigua*, and *S. lasiolepis*.

The mesquite, *Prosopis*, attains its best development on the alluvial bottomlands throughout the Southwest, but is also present on the Mohave and Colorado Deserts. Among its associates in desert areas which are represented by Mount Eden equivalents are: *Prunus andersonii*, *P. fremontii*, *Ephedra* spp., *Salix exigua*, *Lepidospartum squamatum*, and *Sapindus drummondii*. *Prosopis* is uncommon in the arid portions of interior southern California. West of Beaumont, in the arroyos of San Timoteo Canyon, mesquite has been noted with the following species which are represented by fossil equivalents in the Mount Eden flora: *Arctostaphylos glauca*, *Ceanothus cuneatus*, *Cercocarpus betuloides*, *Lepidospartum squamatum*, *Platanus racemosa*, *Salix exigua*, and *S. lasiolepis*.

The desert peach, *Prunus andersonii*, is distributed along the western edge of the Colorado and Mohave Deserts, and ranges northward on the east front of the Sierra Nevada Mountains in a typical Great Basin habitat. In southern California desert peach was noted with typical desert shrubs, as well as with *Ephedra*, *Prosopis*, *Salix*, and *Lepidospartum*. The general implications are of at least desert-border conditions existing throughout its southern range.

Prunus fremontii grows on the slopes adjoining the Colorado Desert, where it is associated with yuccas and desert shrubs. Desert apricot also occurs near the mouth of Whitewater Canyon, 15 miles east of Beaumont on the edge of the Colorado Desert. The following species which have Mount Eden representatives grow near *Prunus fremontii* at this locality: *Arctostaphylos glauca*, *Ceanothus divaricatus*, *Cercocarpus betuloides*, *Lepidospartum squamatum*, *Platanus racemosa*, *Salix exigua*, and *S. lasiolepis*. Several miles farther up the canyon *Quercus chrysolepis*, *Pinus coulteri*, and *Pseudotsuga macrocarpa* are present on north slopes. Both *Ephedra* and *Prosopis* are abundant on the desert at the mouth of this canyon. The present plant association of this area, representing 43 per cent of the living equivalents of the flora, could probably enter a sedimentary record if conditions favorable for preservation were present. The canyon was visited in the spring when rains had swollen the stream into a torrent, so that the manner of present leaf deposition could not be observed. All of the above species, however, were noted along the edges of the creek at some point in the canyon, so that their leaves and fruits could readily be lodged at the sites of deposition.

Although usually a component of the xeric chaparral throughout the San Jacinto Mountains and southward into Mexico, *Quercus palmeri* may also border desert areas. This scrub oak has been noted in association with all of the other California species of the desert-border element.

Sapindus has been included in the desert-border unit because in the Southwest and in Sonora it grows well out into the desert scrub along stream courses. Among its typical associates are species of *Ephedra*, *Juglans*, *Platanus*, *Populus*, *Prosopis*, and *Salix*.

From the preceding discussion it is apparent that the desert-border unit occupied exposed dry slopes in the Mount Eden basin. Such areas were afforded by the steep granitic hills against which the sediments were deposited. This xeric association may have been present, but to a lesser extent, on the lower exposed slopes bordering the basin. That such areas were existent is suggested by the abundance of *Pinus pretuberculata*, *P. pieperi*, and *P. hazeni* in the flora, since their living equivalents are typical of arid habitats.

Following this consideration of the ecologic occurrence of the desert-border element, it seems desirable to account for the present distribution of this xeric association in the area to the east of the fossil locality. The climatic

trend in southern California since the Pleistocene has been toward a warmer and drier climate than that which prevailed in that region during the Pliocene. The wide-spread expansion of desert areas is indicative of this climatic change. In addition, studies of the digger pine forest suggest that winter temperatures in interior southern California are approximately 8 degrees higher than those which obtained in that area in the Pliocene.

Vertebrate evidence indicates that this climatic trend was accompanied by wide-spread chaparral expansion, and this scrub formation has apparently supplanted areas of the desert-border unit in the Beaumont area. The relict occurrence of *Prosopis juliflora* var. *glandulosa*, *Chilopsis linearis*, *Yucca mohavensis*, *Ephedra nevadensis*, and *Coleogyne ramosissima* on dry exposed slopes in the Mount Eden area supports this suggestion, for they are all typical of desert regions. In view of the presence of these species in the Mount Eden area, it seems likely that the living equivalents of the desert-border element could probably exist in exposed situations in that region today, were chaparral not the dominant scrub formation. In interior southern California chaparral is a rapid and aggressive invader into all vegetative types, and, once established, is quickly stabilized. Relict occurrences of former more wide-spread plant associations may be found throughout the chaparral in southern California. Among these may be mentioned isolated areas of grassland, oak, walnut, big-cone spruce and Coulter pine, digger pine, and, as indicated above, desert-border shrubs. Thus, it seems apparent that the desert-border association was confined to the edge of the present Colorado Desert, 15 miles east of the Mount Eden area, in response to an invasion by a more virile plant formation.

Sapindus, on the other hand, is now distributed from southern Arizona to Kansas and southward into Sonora, Mexico. This area is one of summer rainfall, whereas in southern California precipitation is limited to the winter season. *Sapindus* was evidently eliminated from California in response to a shift from a climate of some summer rainfall and a winter maximum, to a climate of dry summers, with precipitation restricted to the winter season. It is also possible that the chaparral formation may to some extent have displaced relict areas of *Sapindus* in southern California.

Lake-border or Marsh

The geologic evidence indicates the presence of lakes in the Mount Eden basin, and this is further corroborated by the presence of the typical marsh and lake-border genera, *Typha* and *Equisetum*, in the flora. Chaney has noted a correlation between arid climate and the accumulation of sediments in shallow lakes,¹ and the Mount Eden flora further supports this suggestion. Many of the riparian species may also have occupied the borders of lakes and marshes in the Mount Eden basin during the Pliocene.

¹ Svenska Sällskapet för Antropologi och Geografi, Geografiska Annaler, Sven Hedin, 1935.

Riparian

The riparian element denotes a stream-bank habitat, and in interior southern California this ecologic unit constitutes the typical arborescent growth throughout the lower altitudes, for the adjacent slopes are covered by chaparral.

FOSSIL SPECIES AND MODERN EQUIVALENTS OF THE RIPARIAN ELEMENT

Fossil species	Modern equivalents
<i>Fraxinus edensis</i>	<i>Fraxinus dipetala</i>
<i>Juglans beaumontii</i>	<i>Juglans californica</i>
<i>Lepidospartum</i> sp.	<i>Lepidospartum squamatum</i>
<i>Platanus paucidentata</i>	<i>Platanus racemosa</i>
<i>Populus pliotremuloides</i>	<i>Populus tremuloides</i>
<i>Salix coalingensis</i>	<i>Salix lasiolepis</i>
<i>Salix</i> sp.	<i>Salix exigua</i>
<i>Sapindus lamottei</i>	<i>Sapindus drummondii</i>

Fraxinus is a small tree or large shrub and is a common stream-bank associate in southern California, but usually does not grow along streams in the lower chaparral and sagebrush areas. This ash is primarily an important constituent of the chaparral on north slopes, where it is usually associated with *Arctostaphylos*, *Ceanothus*, *Cercocarpus*, and shrubby *Quercus* species.

Platanus, *Lepidospartum*, and *Salix* are characteristic riparian elements throughout southern California, and the latter two are well developed along watercourses in desert areas. Although sycamore may approach deserts along permanent streams, it generally does not follow drainages into the desert proper, as do *Lepidospartum squamatum* and *Salix exigua*.

Juglans reaches an optimum development under the influence of coastal breezes and fogs on the western slopes of the Santa Ana Mountains and in the Puente Hills, where it forms extensive savanna-woodland associations. The California walnut is confined to stream banks in the more arid portions of its range, as in interior southern California, where it is of local occurrence. East of San Bernardino in Devil's Canyon and in Waterman Canyon, isolated clumps of *Juglans* are associated with the following species which have Mount Eden equivalents: *Arctostaphylos glauca*, *Ceanothus cuneatus*, *C. divaricatus*, *Cercocarpus betuloides*, *Fraxinus dipetala*, *Lepidospartum squamatum*, and *Salix lasiolepis*; *Pinus coulteri*, *Pseudotsuga macrocarpa*, and *Quercus chrysolepis* are present a short distance farther up the canyons.

In view of the abundance of walnut fruits, and the presence of only a single leaflet in the flora, it is believed that *Juglans* was confined to stream banks or to edges of marshes or lakes in the Mount Eden basin. This is consistent with evidence indicative of an arid climate in the Mount Eden basin, where leaves would be dried and decayed by the sun and wind before entering a sedimentary record. Although vertebrate evidence supports the presence of savanna associations in the Mount Eden area in the Pliocene, the

extent of development of *Juglans* in them is conjectural. Since the abundance of xeric associations in the flora suggests that the Pliocene marine embayment to the west had no great effect on the flora in the Mount Eden basin, and because walnut reaches optimum development in the cooler coastal area, it seems likely that *Juglans* was not widely developed in savanna associations.

It may be stated that while *Juglans* was present in savanna formations, it was probably not common, and that the abundance of fruits in the flora is primarily indicative of a riparian habitat in an arid climate where leaves would be destroyed before entering the sedimentary record. The several small areas of walnut in interior southern California, which are now confined to stream banks, are apparently relicts of a former more wide-spread Pliocene association. The disappearance of *Juglans* from the Beaumont area seems directly related to the increasing aridity and rising temperatures throughout that region. Chaparral has also displaced occasional areas of walnut in interior southern California.

The presence of *Populus pliotremuloides* in the flora is only an apparent anomaly. Although its living equivalent, *P. tremuloides*, is usually limited to higher elevations throughout the mountains of western America, this aspen has also been noted in semiarid regions. Mason¹ and Condit² have observed *Populus tremuloides* at lower altitudes in Nevada in a semiarid habitat, and Goldman has reported a similar occurrence in Baja California.³ In addition, Sudworth⁴ has noted aspen in semiarid areas in eastern Oregon and in California "in dry places with mountain mahogany [*Cercocarpus*] and other chaparral." This species grows in such areas along cold streams, or in deep canyons with descending currents of cold air. The abundance of aspen in the flora suggests similar conditions of growth for the Pliocene species, and its present absence from the Mount Eden area is probably due to topographic features which do not favor such irregularities in local distribution. Its nearest modern occurrence is 20 miles north of the fossil area, at an elevation of 7000 feet in the San Bernardino Mountains.

As stated in the discussion of the desert-border unit, *Sapindus* is a typical riparian species throughout its range, and may approach deserts along water-courses in the Southwest.

Savanna and Woodland

The savanna-woodland unit forms open woodland-grass associations in drier areas, and in more favorable localities, especially on north slopes, the same species may comprise woodland types.

¹ Oral communication, October 15, 1935.

² Oral communication, October 18, 1935.

³ Contr. U. S. Nat. Herb., vol. 16, pt. 13, 319, 1913.

⁴ *Forest Trees of the Pacific Slope*, 243, 1908.

**FOSSIL SPECIES AND MODERN EQUIVALENTS OF THE
SAVANNA-WOODLAND ASSOCIATION**

Fossil species	Modern equivalents
<i>Arbutus</i> sp.....	<i>Arbutus xalapensis</i>
<i>Juglans beaumontii</i>	<i>Juglans californica</i>
<i>Pinus pieperi</i>	<i>Pinus sabiniana</i>
<i>Quercus hannibali</i>	<i>Quercus chrysolepis</i>
<i>Quercus lakevillensis</i>	<i>Quercus agrifolia</i>
<i>Quercus orindensis</i>	<i>Quercus douglasii</i>

Arbutus sp. represents a Sonoran element which is no longer found in California and constitutes an upland element in the Mount Eden flora. *Arbutus xalapensis*, which closely resembles the Mount Eden species, is distributed from western Texas southward through Mexico. Standley¹ recognizes some 10 described species of *Arbutus* as being only variants of one species, *A. xalapensis*. Those to the north have smaller leaves than the Mount Eden species and are entire-margined; they include such types as *A. petiolaris*, *A. mollis*, and *A. prunifolia*. These northern forms are typical of a semiarid habitat and may be associated with juniper, pinyon pine, xeric oaks, *Yucca*, *Cercocarpus*, and other shrubs of dry habitats. In the Mexican Plateau, *A. xalapensis* includes *A. macrophylla*, *A. varians*, and *A. densiflora* among its variant forms, and is associated with black oak, chestnut oak, *Carya*, *Juglans*, *Vitis*, *Alnus*, *Smilax*, and *Bauhinia*. This latter association, which grows at higher elevations, is indicative of a greater rainfall and less extremes of temperature. The leaves of these more mesic types resemble the Mount Eden species more closely than do the xeric forms to the north, which are smaller and are entire-margined. The Mount Eden species is evidently an expression of a cool moist habitat, rather than one of semi-aridity, and is believed to represent an upland element in the flora.

In connection with the disappearance of this Mexican madrone from the California flora, it is highly significant that the writer has discovered a madrone in a Miocene flora near Tehachapi, California. This *Arbutus* is also referable to *A. xalapensis*, and is similar to the Mount Eden species. The Miocene flora is definitely Mexican in its affinities, and it seems certain that the climate of that epoch was characterized by summer rainfall. It may be suggested that the Pliocene madrone is a relict occurrence of a former more wide-spread Miocene species, and was near the border of its range in the Pliocene. Its segregation from the California flora is apparently related to a shift in the seasonal distribution of rainfall. During the Miocene in southern California, *Arbutus* thrived in a climate with summer rainfall. In the Middle Pliocene it was an upland element in the Mount Eden flora and lived in a climate with some summer rainfall, but with maximum precipitation confined to the winter season. Today, however, it is limited to Mexico in an area with summer rainfall, and this is apparently in direct re-

¹ Contr. U. S. Nat. Herb., vol. 23, pt. 4, 1100, 1924.

sponse to the present California climate with its precipitation limited to the winter season.

Arbutus xalapensis is distinct from the larger-leaved *A. menziesii* of the Pacific states, whose fossil equivalent, *A. matthesii* Chaney, has been widely recognized in the later Miocene floras of northeastern California, eastern Oregon and Washington, and adjacent Idaho. This madrone has been associated with a border redwood forest since the Miocene, and Dorf¹ has reported an *Arbutus* referable to *A. menziesii* in the California Pliocene growing with a similar assemblage. As already stated, *A. xalapensis* is only known from one Miocene flora, and this is on the edge of the Mohave Desert near Tehachapi. The associated flora is a Sonoran plateau element composed of palm, pinyon pine, xeric oaks, cottonwood, willow, and arborescent legumes. The palæontologic relations of these two madrones are conjectural at the present time. *A. xalapensis* may be a southern Tertiary segregate of an *A. matthesii* type, in response to greater aridity in the south. On the other hand, the Sonoran species may represent a northward Tertiary extension of a flora now confined to the Mexican plateau.

Juglans comprises wide-spread savanna associations in the cooler coastal area on the western slopes of the Santa Ana Mountains, and in the Puente Hills. As walnut is believed to have formed a riparian association in the Mount Eden basin, it was considered with the other species of that unit. Although vertebrate evidence indicates the presence of savannas in the Mount Eden area in the Pliocene, the extent of development of *Juglans* in that association was probably not very great.

Quercus agrifolia is common throughout the valleys and foothills of the Coast Ranges of California and extends into Baja California. Increasing aridity may be a factor accounting for its present scarcity in interior southern California, for it reaches optimum development near the coast.

The presence of *Quercus hannibali*, the Pliocene equivalent of *Q. chrysolepis*, in the flora is indicative of an upland element. In southern California this oak is commonly associated with big-cone spruce, Coulter pine, and the upper chaparral element. It occasionally reaches lower altitudes in cool canyons, and in favorable areas may form dense woodlands.

The Digger Pine Forest

Many Pleistocene floras of California indicate a southward movement of their equivalent modern forests, and are to be correlated with the southward shift of isotherms and increasing humidity accompanying glaciation. The recent trend to aridity, with attendant rising temperatures, has resulted in a northward restriction of these floras, and a warmer and drier climate now characterizes those areas which they occupied during the Pleistocene. The northward movement of the digger pine forest from the Pliocene Mount

¹ Carnegie Inst. Wash. Pub. No. 412, 54, 1930.

Eden, San Timoteo, Pico,¹ and San Fernando ² localities, as well as from the Pleistocene Carpinteria ³ locality, is consistent with this general migration. The fossil localities of digger pine and the closest occurrence of the living forest to the various areas are as follows:

Pliocene occurrence	Nearest digger pine forest to fossil area
Mount Eden.....	Pine Creek, Antelope Valley, 100 miles north
San Timoteo.....	Pine Creek, Antelope Valley, 100 miles north
Pico	Santa Ynez Mountains, 40 miles north
San Fernando.....	Antelope Valley, 25 miles north
Pleistocene occurrence	
Carpinteria	Santa Ynez Mountains, 30 miles north

It is of interest to note that on Pine Creek along the southern edge of Antelope Valley, which is the most southern occurrence of the digger pine forest, many of the associates of digger pine are also represented by equivalent species in the Mount Eden flora. Among these may be listed:

Arctostaphylos glauca	Prosopis juliflora var. glandulosa
Ceanothus cuneatus	Prunus andersonii
Ceanothus divaricatus	Pseudotsuga macrocarpa
Cercocarpus betuloides	Quercus chrysolepis
Ephedra spp.	Quercus douglasii
Fraxinus dipetala	Salix exigua
Lepidospartum squamatum	Salix lasiolepis
Platanus racemosa	

Northward, as one passes from the border of the southern California province, the associates of digger pine which have Mount Eden correlatives rapidly decrease in number.

Digger pine, the living equivalent of *Pinus pieperi*, is commonly represented in a *Pinus-Quercus* association, and *Quercus douglasii*, whose Pliocene equivalent is *Q. orindensis*, is its typical associate. These two modern species form a savanna association about the Great Valley of California, and reach optimum development in the foothills of the central Sierra Nevada. The forest is characterized by hot, dry summers, and the soil commonly bakes and cracks during the summer drought. The rainy season lasts from November into April and the winters are cold.

Before proceeding with the climatic interpretation of the forest, the maritime occurrence of *Pinus pieperi* in the Pico and Carpinteria deposits must be considered, for digger pine is an arid interior element in the present California flora. The presence of digger pine in the coastal flora at Carpinteria may be attributed to distant slopes which were subject to greater extremes of temperature than obtained on the immediate coast. The bat-

¹ Dorf, Carnegie Inst. Wash. Pub. No. 412, 56, 1930.

² A cone deposited in the Los Angeles Museum, which was collected 25 miles north of Los Angeles, near San Fernando, is evidently of Pliocene (Fernando) age.

³ Chaney and Mason, Carnegie Inst. Wash. Pub. No. 415, 74, 1930.

tered condition of the cone scale representing this species in the flora is in accord with the suggestion of transportation from an inland locality.¹ The cone material of the Pico florule, 6 miles north of Ventura, is in a marine deposit directly along the present coastline; two carbonized cones of *Pinus masoni* are also present in the florule. *Pinus muricata*, the living representative of *P. masoni*, is coastal in distribution today, while digger pine is typically interior. This is suggestive of either (a) the presence of *Pinus pieperi* along the Pliocene coast of southern California, or (b) the occurrence of that pine on arid slopes some distance from the coast, and subsequent transportation to a marine site of deposition, or (c) the presence of a marine embayment during the Pliocene which extended inland and was sheltered by mountains, now eroded away, on the leeward slopes of which arid sites prevailed. Digger pine is not coastal in distribution today, and there is no reason to assume such a habitat for its Pliocene equivalent, for *Pinus muricata* and digger pine do not approach each other in distribution. The writer, however, has observed both of these conifers growing 30 miles apart along the Santa Ynez River. *Pinus muricata* occurs near the coast at the mouth of the river, while digger pine grows along the same river farther inland. It seems possible that cones of these two species might readily mingle at a coastal site of deposition. The writer has noted cones of digger pine in the Sisquoc River which were transported to within 8 miles of the ocean from a point 25 miles distant from the nearest digger pine. It is not to be doubted that occasional cones have reached the ocean following heavy spring rains. For this reason, it is believed that the material of the Pico florule was transported from an inland area to the coast, or, possibly, that it grew on arid leeward slopes of a mountain range, now removed by erosion, which was bordered by a marine embayment.

In applying climatic data to an interpretation of the Pliocene and Pleistocene floras of California, two definite climatic areas are to be contrasted, one an interior, and the other a coastal phase; the Mount Eden flora is definitely an interior association. In California, the effective moisture relationships of fog and rainfall are of greater significance to coastal than to interior floras. The importance of fogs in influencing the distribution of coastal floras has been illustrated by Chaney and Mason in their study of the Monterey pine forest.² Temperature changes, however, are apparently more critical to interior floras, and this is consistent with the climatic implications of the digger pine forest. There is a gradual southward decrease in rainfall for 400 miles through the forest, varying from 53 inches in the north to 10 inches annually near the southern border of the forest; temperatures vary but little over the same area. Thus, while the northward movement of the Pleistocene floras of southern California is paralleled by a similar movement of the digger pine forest, these two migrations are related to

¹ Chaney and Mason, Carnegie Inst. Wash. Pub. No. 415, 56, 1930.

² *Ibid.*, 75, 1930.

different causes. One is a coastal phase in which the effective moisture relation is critical, and the other an interior association in which temperatures are significant.

For an approximation of the climatic conditions of the digger pine forest, a table was prepared from climatic data gathered at 37 meteorological stations throughout the range of the forest.¹ The annual rainfall was found to vary greatly at the northern and southern limits of the forest. In the northern end of the Great Valley, at Shasta, the yearly precipitation is 53 inches. Rainfall decreases steadily southward through the Valley, and at Caliente, which is at the southeastern corner of the Great Valley and 400 miles south of Shasta, the annual precipitation is only 10 inches. It is obvious that with such a lateral variation in rainfall, an average for the forest would be of no significance.

Temperatures, however, vary but little throughout the same area and at the majority of the stations were within 2 or 3 degrees of the averages in-

TABLE 2—Average temperature data for the digger pine forest and for areas of former digger pine occurrence *

	Average temperatures			Temperature extremes	
	Year	3 mo. summer	3 mo. winter	High	Low
Digger pine forest.....	59.4°	91.4°	35.2°	112°	11°
Areas of former digger pine occurrence.....	63.4	91.9	44.2	113	19

* Temperatures were not included for the coastal stations, for digger pine is an interior rather than a coastal element of the California flora.

indicated in table 2. Those stations with any significant departures from these averages were in all cases located at elevations of over 3000 feet, near the upper limits of the forest. As might be expected, these temperatures were lower than the average for the forest.

Higher temperatures are present in areas of the former distribution of digger pine than now obtain in the forest to the north. From the data in table 2 it is apparent that there is a significant discrepancy in winter temperatures. Average winter temperatures are 9 degrees higher in areas of former digger pine occurrence than in the forest to the north, and extreme temperatures for the same season exceed those of the digger pine forest by 8 degrees. Of equal significance is the fact that summer temperatures are nearly identical in both areas. It thus appears that winter temperatures are of critical importance in determining the distribution of digger pine.

¹The data were obtained from the U. S. Weather Bureau, "Climatic Summary of the United States," secs. 15-18, 1930, and from the files of the U. S. Weather Bureau Office in San Francisco, California. All temperature data are Fahrenheit.

In interpreting climatic data with regard to the critical season influencing the responses of plants and animals, MacGinitie¹ and Taylor² have illustrated the fact that the extremes of temperature are more significant than the means. It is the occasional season of the year, or the most critical year or years of a climatic cycle, wherein a critical factor is in excess of the tolerance of a species for a particular factor, that often governs the distribution of the species.³ The higher winter temperatures in southern California evidently exceed the tolerance of digger pine. Thus, this association has apparently been segregated from the southern California flora in response to rising winter temperatures in that area since the Pleistocene.

In addition, the following point may be mentioned as having a direct bearing on the problem of digger pine distribution. In southern California chaparral is an aggressive and active invader into grass, savanna, woodland, and lower forest areas following fire, and, once established, is quickly stabilized. The lower and middle mountain slopes in interior southern California are completely dominated by this formation. Only in the coastal region, and on the western boundary of interior southern California along the larger river valleys which have moderating oceanic breezes during the summer, are plant associations other than chaparral developed to any considerable extent at lower elevations. It is not unreasonable to suppose that in southern California, the center of chaparral distribution and the area of its greatest development, such a virile climax could readily supplant any relict areas of digger pine. A lone digger pine and several trees of *Quercus douglasii* on Piru Creek, 20 miles southwest of the southern limit of the forest, constitute such a relict. This locality is definitely within the southern California province. Growing in a large chaparral area, this relict will sooner or later be destroyed by fire. The subsequent invasion of the area by chaparral demonstrates the process of elimination and restriction of an older element by a more virile climax.

In summary of the digger pine problem, the following conclusions seem justified:⁴ (1) Since Mount Eden time there has been a northward movement of the digger pine forest. It may be suggested that rising winter temperatures in southern California since the Pleistocene are in part responsible for its northward migration. (2) Wide-spread chaparral expansion is of late Quaternary development in southern California, and such areas of digger pine as may have continued after that epoch have been gradually displaced by this scrub formation.

¹ Science, n.s., vol. 78, 190, 1933.

² Ecology, vol. 15, 374-379, 1934.

³ Mason, Madroño, vol. 3, no. 5, 1936.

⁴ Dr. H. L. Mason has recently reported to the writer the occurrence of a digger pine cone in Pleistocene deposits near San Jacinto. This record is in accord with both conclusions.

Chaparral

Chaparral species are common in the Mount Eden flora and most of their living equivalents are important constituents of this formation throughout southern California. Chaparral is not as widely developed in the coastal area as in interior southern California. Although it is dominant in the coastal region, large areas of grassland, savanna, and woodland are present, and coastal sagebrush is climax locally. The scrub formation is a rapid and aggressive invader into all vegetative types in interior southern California, and, once established, is evidently stable. Other than chaparral, plant associations of any considerable extent in interior southern California are only to be found along the large river valleys which have cool, ameliorating oceanic breezes most of the summer, or in the higher mountains.

It seems evident that the trend to a warmer and drier climate in southern California since the Pleistocene, coupled with recurring fires, has favored chaparral expansion in the interior area. In this connection, it is significant that chaparral reaches optimum development in drier and warmer interior southern California, rather than in the cooler coastal area. Vertebrate evidence suggests that wide-spread chaparral development did not take place before the Quaternary.

FOSSIL SPECIES AND MODERN EQUIVALENTS OF THE CHAPARRAL UNIT

Fossil species	Modern equivalents
<i>Arctostaphylos preglauca</i>	<i>Arctostaphylos glauca</i>
<i>Arctostaphylos prepungens</i>	<i>Arctostaphylos pungens</i>
<i>Ceanothus</i> sp.....	<i>Ceanothus cuneatus</i>
<i>Ceanothus edensis</i>	<i>Ceanothus divaricatus</i>
<i>Cercocarpus cuneatus</i>	<i>Cercocarpus betuloides</i>
<i>Fraxinus edensis</i>	<i>Fraxinus dipetala</i>
<i>Quercus pliopalmeri</i>	<i>Quercus palmeri</i>
<i>Rhus prelaurina</i>	<i>Rhus laurina</i>

All of the above species are typical components of the chaparral formation in southern California. Of these, only *Quercus palmeri* and *Rhus laurina* are indicative of conditions which seem worthy of mention, for they represent two extremes of chaparral tolerance. *Quercus palmeri*, whose fossil equivalent is one of the dominant species of the flora, often approaches desert areas, and has been noted in association with *Prunus fremontii*, *Ephedra*, and *Prosopis* on the slopes of the Colorado Desert. This scrub oak is the most xeric of the chaparral species with fossil equivalents in the Mount Eden flora.

In marked contrast to the scrub oak, *Rhus laurina* is indicative of cooler conditions. This latter species is uncommon in interior southern California, and reaches optimum development in the coastal area. It approaches the interior region only along the larger river valleys which have cool oceanic breezes most of the summer. The disappearance of *Rhus* from the Mount

Eden area is also apparently related to increasing aridity in that interior region.

The absence of chamise (*Adenostoma fasciculatum*) in the flora is particularly noteworthy, for it is the most abundant and wide-spread chaparral species in southern California. Through all of southern California on the lower and middle slopes of the mountain ranges *Adenostoma* is the dominant chaparral element. At higher elevations it is subordinate to *Arctostaphylos*, *Ceanothus*, and shrubby *Quercus* species. The hazards involved in its preservation are perhaps too great to have permitted its incorporation in the sediments containing the Mount Eden flora, for the small linear leaves are readily broken and crushed. The presence of many chaparral and arborescent species in the flora, all of which are the typical associates of chamise today, would suggest that it was present in the Mount Eden area.

Coniferous Associations

Conifers which may now be found on the upper slopes in the Sierra Peak and City Creek areas are represented by equivalent species in the Mount Eden flora.

FOSSIL SPECIES AND MODERN EQUIVALENTS OF THE CONIFEROUS ELEMENT

Fossil species	Modern equivalents
<i>Cupressus preforbesii</i>	<i>Cupressus forbesii</i>
<i>Pinus hazeni</i>	<i>Pinus coulteri</i>
<i>Pinus pretuberculata</i>	<i>Pinus tuberculata</i>
<i>Pseudotsuga premacrocarpa</i>	<i>Pseudotsuga macrocarpa</i>

Coulter pine (*Pinus coulteri*) and big-cone spruce (*Pseudotsuga macrocarpa*) are well represented by their fossil equivalents in the Mount Eden flora. Big-cone spruce is typical of protected north gulches and canyons throughout southern California at middle elevations, and occasionally extends into the lower chaparral in favorable canyons as small clumps and thin stringers. Coulter pine may grow with big-cone spruce, but is characteristic of exposed ridges and drier slopes and flats. Both Coulter pine and big-cone spruce extend into Baja California. The former occurs farthest northward, being found on the upper edge of the digger pine forest scattered through the higher mountain ranges as far north as Mount Diablo, 25 miles east of San Francisco Bay. The northern range of big-cone spruce is in the San Rafael Mountains and it is endemic to southern and Baja California.

Two cones in the Mount Eden flora are referable to *Cupressus forbesii*, a species which has its major distribution in San Diego County. The northernmost occurrence of this cypress is on the north slope of Sierra Peak, where over 60 per cent of the living equivalents of the Mount Eden flora may be found.

Pinus tuberculata has a wider geographic distribution than any of the other living representatives of the conifers in the Mount Eden flora. Knob-cone pine is typical of dry exposed ridges on poor and rocky soils from southern Oregon to Baja California. In the City Creek area (Plate 1, fig. 2) the majority of its associates are also represented by equivalent species in the Mount Eden flora. Among these are *Arctostaphylos glauca*, *Ceanothus cuneatus*, *C. divaricatus*, *Cercocarpus betuloides*, *Fraxinus dipetala*, *Pinus coulteri*, *Pseudotsuga macrocarpa*, and *Quercus chrysolepis*. Lower down in the canyon *Platanus racemosa*, *Salix exigua*, and *S. lasiolepis* are present, while in more open situations *Lepidospartum squamatum* grows with the riparian species.

It seems justified at this point to comment on the conspicuous coniferous element in the Mount Eden flora, for these species comprise nearly half of the total material represented in the flora. The abundance of conifers in the flora suggests that during the Pliocene they were growing at lower elevations than their typical equivalent associations which are now to be found in southern California. It is significant that the lithology of the sediments and the botanical relations are both consistent with this assumption.

In examining present conditions of deposition of plant material along the desert side of the San Jacinto and San Bernardino Mountains, as well as on the western slopes of these mountains, the writer has noted that vegetation obtained from upland areas is associated with coarse, unsorted, conglomeratic deposits. Cones of *Pseudotsuga macrocarpa* and *Pinus coulteri* have been observed in desert washes 15 miles from the nearest group of these trees. During the normal flow of the streams, however, plants associated in the finer deposits are derived from areas close to the site of deposition. It may be added that Mason¹ has noted a similar type of deposition along Waddell Creek in the Santa Cruz Mountains. As the Mount Eden beds are principally composed of fine sandstones and shales, it seems evident that the lithology is consistent with the assumption that the living upland coniferous species in southern California, representing Mount Eden conifers, prevailed at lower elevations during that epoch than at present.

Detailed distributional studies on the occurrence of *Pinus coulteri* and *Pseudotsuga macrocarpa*, both of which are abundantly represented by equivalent species in the Mount Eden flora, further substantiate the former presence of these species at lower elevations. Relict areas of these conifers may be found in cool, favorable canyons in southern California at lower elevations. It is significant that these areas are well below the present typical forests, and that the intervening slopes are completely dominated by chaparral. The scrub formation has supplanted extensive areas of these coniferous associations which formerly prevailed at lower altitudes. The development of chaparral throughout the lower mountain slopes at the expense of the conifers has been favored by increasing aridity and rising tem-

¹ Carnegie Inst. Wash. Pub. No. 415, 134, 1934.

peratures, as well as by recurring fires, in interior southern California. Since vertebrate evidence indicates that vegetation suited to plains-savanna mammals existed well into the Pleistocene, it seems evident that wide-spread chaparral expansion is of late Quaternary development in interior southern California. Hence, the conifers have apparently been supplanted by chaparral at lower elevations since that time.

SUMMARY OF THE PHYSICAL CONDITIONS SUGGESTED BY THE FLORA

The habitat conditions suggested by the modern equivalents of the flora, and as further substantiated by both geologic and vertebrate evidence, are indicative of a low-lying basin occupied by shallow lakes and marshes, with adjacent highlands. Around the lake borders and in the marshy areas was a typical hydric element of *Typha* and *Equisetum*. Riparian species of *Platanus*, *Salix*, and *Juglans* were also present and extended well up into the adjacent hills along stream courses; *Populus* was probably confined to cooler canyons. On the lower portions of alluvial fans, in drier watercourses, and on lower exposed slopes was a desert-border element of *Ephedra*, *Prosopis*, *Prunus* spp., and *Sapindus*. A savanna of *Quercus* spp., *Pinus pieperi*, and to a lesser extent *Juglans*, existed over the rolling hills and plains, and on more favorable north slopes these same species formed woodland associations. This savanna-woodland was locally interrupted by chaparral species of *Arctostaphylos*, *Ceanothus*, *Cercocarpus*, *Rhus*, and *Fraxinus*. A coniferous element existed above the savanna-woodland, and was at lower elevations so that cones could be readily transported to sites of deposition. *Pseudotsuga* reached optimum development on cooler north slopes, while the other species were characteristic of drier exposures.

A critical analysis of the modern equivalents of the Mount Eden flora affords evidence relative to the climatic conditions which obtained in the Mount Eden area in the Pliocene.

1. In view of the abundant development of xeric associations in the Mount Eden flora, it seems apparent that the ameliorating influences of the Pliocene embayment in the area to the west and north were not very great, for the flora is distinctly an interior association.

2. The occurrence of *Sapindus* and *Arbutus* in the flora indicates that the Mount Eden area probably received some summer rainfall. However, since the rest of the flora now prevails in an area of winter rainfall, it is quite likely that the summer precipitation was inappreciable. Rainfall in the Mount Eden region increased with elevation. While the desert-border element now prevails in areas of rainfall below 10 inches, *Pseudotsuga* and Coulter pine suggest an annual precipitation approaching 25 or 30 inches.

3. A study of the digger pine forest indicates that the present winter temperatures in the Mount Eden area are higher than those which obtained in the same area in the Pliocene. It is difficult to present temperature data

for the rest of the flora, for temperature, as well as rainfall, varied with increasing elevation in the successive habitat associations represented in the flora.

Supplementing this ecologic aspect of the flora, the following points afford a summary of the conditions which apparently account for the changing floral composition in the Mount Eden area since the Pliocene:

1. The northward movement of the digger pine forest seems to be correlated with rising winter temperatures in southern California since the Pleistocene.

2. The several isolated areas of walnut which are confined to stream banks in interior southern California are relict occurrences of a former more widespread Pliocene association. The disappearance of *Juglans* from the Mount Eden area is directly related to the increasing aridity in that interior region.

3. The Pliocene and Pleistocene vertebrate faunas of the Mount Eden region contain plains-savanna mammals, and thus indicate that wide-spread chaparral expansion is of late Quaternary origin in interior southern California. The recent trend to a warmer and drier climate, in addition to continued fires, has evidently favored the development of this scrub formation. Chaparral has supplanted areas of the desert-border unit in the Mount Eden area, as well as coniferous associations which formerly occupied lower slopes, and savanna-woodland associations of walnut and digger pine in interior southern California.

4. The Sonoran element of *Arbutus* and *Sapindus* was apparently segregated from the flora in response to a change in the seasonal distribution of rainfall.

AGE OF THE FLORA

In determining the age of the flora, four lines of evidence will be considered: (1) the vertebrates associated with the flora, (2) the numerical representation of Mount Eden species in floras of known geologic age, (3) the climatic and ecologic aspects of the flora as compared with California floras of definite age, and (4) the distributional aspects of the Mount Eden flora as related to other floras of definite stratigraphic position. Before discussing the indications of the plants regarding the age of the Mount Eden beds, the significance of the mammals will be briefly reviewed.

1. The vertebrate fauna of the Mount Eden beds was originally believed by Frick¹ to be of late Lower Pliocene age; subsequently he referred it to the uppermost Pliocene.² Simpson,³ in correlating the North American Tertiary mammal-bearing formations, questionably indicates a Middle Pliocene age for the Mount Eden beds. In a recent consideration of the "Succession of the North American Continental Pliocene Mammalian Faunas," Stirton⁴ has designated the Mount Eden fauna as of late Middle Pliocene age.

¹ Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 12, No. 5, 287, 1921.

² Bull. Amer. Mus. Nat. Hist., vol. 59, art. 9, 516, 1933.

³ Bull. Amer. Mus. Nat. Hist., vol. 67, art. 3, 1933.

⁴ Amer. Jour. Sci., vol. 32, 174, 1936.

It is apparent that the beds are definitely of Pliocene age, but their position in that epoch is for the present somewhat questionable. Regional comparisons with other faunas seem to favor a Middle Pliocene age, while a Lower Pliocene age is definitely excluded.

2. No typical Miocene plant species are present in the Mount Eden flora; *Typha lesquereuxi* is a wide-ranging Tertiary form of no stratigraphic significance. Of the 30 species of Mount Eden plants, only 9 have been recorded in other California Pliocene floras,¹ and another species (*Cupressus preforbesii*) has been questionably reported. Table 3 shows the distribution of the Mount Eden species among the other Pliocene floras in California.

Since the correlated species of these floras constitute riparian and xeric elements which were wide-spread in the California Pliocene flora, they are of no detailed value in age determination as related to the portion of the epoch in which they occur. It is obvious that the presence of 8 of the 30 Mount Eden species in the Lower Pliocene floras, 3 in the Middle Pliocene assemblage, and 5 in the Upper Pliocene floras of California does not establish any exact stratigraphic horizon. These correlated species were as widely distributed in California during the Pliocene as are their living equivalents. The main botanical elements were, however, of narrow range, just as are their equivalent associations which now grow in California. The redwood forest (Sonoma flora), the broad-sclerophyll and riparian elements (Orinda, Etchegoin, and Alturas floras), the Sierra Transition forest (Santa Clara flora), the coastal conifers (Pico and Merced florules), and the southern California coniferous and chaparral elements (Mount Eden flora) were apparently similar in general distribution during the Pliocene as they are at present. From the discussion concerning the physical conditions, it seems evident that topographic relief influenced the character and distribution of Pliocene vegetation much as it does in California today. The problem of finding a botanical resemblance between Pliocene floras of widely separated areas is as difficult as proving the contemporaneity of the living redwood forest of coastal north-central California and a floral assemblage of southern California.

3. In the following consideration of the botanical evidence the Mount Eden flora will be compared with other California Pliocene floras.

The Ricardo flora of the Mohave Desert is represented by petrified wood, and contains two genera in common with the Mount Eden flora. The *Cupressus* was questionably referred to *C. nevadensis* Abrams, although both *C. forbesii* Jepson and *C. arizonica* Greene were suggested as possible living equivalents. The *Quercus* is of a live oak type and resembles *Q. chrysolepis*, whose Pliocene equivalent is *Q. hannibali*;² this latter species is present in the Mount Eden flora, as well as in several of the floras to the north. Also included in the Ricardo flora are *Pinus kelloggi* (referred to pinyon pine),

¹ Dorf, Carnegie Inst. Wash. Pub. No. 412, 1930.

² Written communication, Mr. L. H. Daugherty, March 1, 1937.

TABLE 3—Distribution of the Mount Eden species in California Pliocene floras

Mount Eden species	Lower Pliocene						Middle Pliocene	Upper Pliocene	
	Wildcat	Merced	Sonoma	Pico	Ricardo	Orinda*	Alturas*	Santa Clara	San Timoteo
<i>Cercocarpus cuneatus</i>	X
<i>Cupressus preforbesii</i>	X	?	X
<i>Pinus pieperi</i>	X
<i>Platanus paucidentata</i>	X	X	X
<i>Quercus lakevillensis</i>	X	X	X	X
<i>Quercus orindensis</i>	X	X
<i>Quercus hambali</i>	X	X
<i>Rhus prelaurina</i>	X	X	X
<i>Salix coalingsensis</i>	X	X	X	X	X
<i>Salix</i> sp.....	X
Total species per flora.....	2	3	4	1	2	6	1	4	1
Number of species by age.....	8						3	5	

* The stratigraphic position of the Orinda and Alturas formations is based on a recent contribution by R. A. Stirton, "Succession of North American Continental Pliocene Mammalian Faunas," Amer. Jour. Sci., vol. 32, 1936.

Palmoxylon mohavensis, and *Robinia alexanderi*. Living vegetation approximating the Ricardo flora now occurs in northern Mexico.

The environmental conditions in the Ricardo area are suggestive of a plains habitat with steep adjacent slopes, and a climate of less extreme aridity than at present. That the mountain slopes of the Mount Eden area were probably cooler than those of the Ricardo region is suggested by the abundant coniferous element of the Mount Eden flora, as well as by the presence of *Arbutus* and *Populus*. The desert-border element of the Mount Eden flora could probably have existed in the Ricardo area, since at the present time both palm and pinyon pine occur in areas adjacent to the modern equivalents of the desert-border species.

Of the Pliocene floras in California, the Lower Pliocene Orinda flora contains 6 of the 30 species represented in the Mount Eden flora, and this is a greater number than is contained in any of the other floras. In both the Mount Eden and the Orinda floras, the riparian and xeric oak species were well developed, and, as evidenced by their distribution, these species were wide-spread in California during the Pliocene. Aside from these similar species, the two floras show no further relationship. A coniferous element is absent in the Orinda deposits, as well as a Sonoran and a desert-border unit; in addition, true chaparral species were not present in the Orinda flora. The dissimilarities between these two floras are on the order of the differences in the modern vegetation in the two regions in which the fossils occur.

Floristically, there is little relation between the remaining California Pliocene floras and the Mount Eden flora. The Lower Pliocene Wildcat and Sonoma floras contain *Sequoia*, and the Merced represents a broad-sclerophyll and riparian assemblage. These floras are indicative of a lower rainfall and higher temperatures existing in those areas than at present, and are suggestive of a more limited distribution of the redwood forest at that time. That the redwood forest was more narrowly confined during the Pliocene, is suggested by the occurrence of a dominant riparian flora (Wildcat) within a typical living redwood forest. Although petrified wood of *Sequoia* and *Pseudotsuga* was found at one locality, this florule, which contains 95 per cent riparian species, is indicative of conditions unfavorable for more than a limited growth of the redwood forest. The Sonoma flora, which contains a conspicuous redwood element, also indicates conditions which were not conducive to optimum development of the redwood forest. The presence of *Quercus orindensis*, *Populus prefremontii*, and *Platanus paucidentata* in the Sonoma assemblage is indicative of higher temperatures and a lower rainfall existing in that area during the Pliocene than at present.

The Middle Pliocene Etchegoin florule, the southernmost of Dorf's interior localities, comprises a dominant riparian element, as well as a xeric oak and a chaparral species. This flora is distinctly interior in aspect and is possibly the most xeric of the floras recorded in northern or central California. It is indicative of conditions more favorable for tree growth than occur at that

fossil locality today, where all of the surrounding area is grassland. Although this florule is quite xeric in aspect, the assemblage which was present in the Mount Eden basin is indicative of greater aridity and higher temperatures than were present in central California.

A prominent Sierra-Cascade element characterizes the Santa Clara flora, and the riparian and broad-sclerophyll units of this assemblage were also well developed. In addition, there is a small representation of the redwood forest. The occurrence of this montane flora at lower elevations is suggestive of cooler conditions than exist in that area today. This is in accord with the general trend toward lowering temperatures in the latter portion of the epoch, prior to the Pleistocene glaciation.

Two maritime florules, each containing 2 species, may be briefly mentioned, for their significance lies in the climatic contrasts which their occurrence suggests were present along the California coastline during the Lower Pliocene. The Pico florule from Ventura contains cone material of *Pinus masoni*, the Pliocene equivalent of *P. muricata* D. Don., and *P. pieperi*, the Pliocene representative of *P. sabiniana* (digger pine). *Pinus muricata* is typically maritime in distribution today, and *P. masoni*, its fossil equivalent, is also presumably indicative of coastal conditions. The presence of *Pinus masoni* with *P. pieperi* at Ventura is suggestive of dry, semiarid slopes approaching the Pliocene coast of southern California, or the transportation of *P. pieperi* to the coast from an inland area of greater aridity.

Pinus masoni was also recorded in the Lower Pliocene Merced sandstones in the sea-cliffs near Mussel Rock, San Francisco, and cones of *Pseudotsuga sonomensis*, which is referable to the modern *P. taxifolia* (Douglas fir), are also present at this locality. The living representatives of these Pliocene conifers are common associates along the coast of north-central California. Their presence in the Merced sandstones is indicative of cooler coastal conditions existing in central California during the Lower Pliocene than were present in the Ventura area some 300 miles to the south at approximately the same time.

The Alturas florule contains *Populus alexanderi*, which is referable to *P. trichocarpa*, and *Salix coalingensis* and points to a region of extensive open, possibly grassy slopes, in which tree growth was confined to stream banks. The very paucity of species in the flora is in itself suggestive of conditions unfavorable for more than a limited forest growth. If a more complete flora were available from this area, it might prove, on the basis of its more interior location, to be indicative of drier conditions than were existent in the Etchegoin florule near Coalinga, California. This florule is demonstrative of the variable aspect of the Pliocene flora of California, depending on its situation in respect to the Pacific Ocean and mountain barriers.

From the preceding consideration of the California Pliocene floras, it is apparent that the vegetation of that period was similar in aspect and general

distribution to that which now prevails in California. While the floras of northern and central California resemble those which exist today in the coastal regions and interior valleys of that portion of California, the Mount Eden flora approximates living vegetation in southern California. The correlated species of these floras constitute riparian and xeric elements which were wide-spread in California during the Pliocene, while the floristic elements typifying each assemblage were of narrow range. The striking botanical changes to be found in areas of high relief and sharp climatic contrasts, as in present-day California, can readily account for such floral diversity. Differences are more apparent than similarities between these Pliocene floras, and they are perhaps of greater significance in determining the later floral history of California.

4. Since the foregoing distributional comparisons of the Pliocene floras of California seem to establish a close relationship between the occurrence of those floras and that of living equivalent vegetation, it now seems desirable to examine critically the Mount Eden flora from the standpoint of the distribution of both the fossil and the living equivalent species. Nearly all of the living representatives of the Mount Eden flora, exclusive of the migrants and those species correlated with other Pliocene floras, are typical of southern California and have not been recorded in the deposits farther north. The living equivalents of the Mount Eden flora which are typical of southern California are listed below. Those species preceded by an asterisk (*) may

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|----------------------------------|--|
| * <i>Arctostaphylos glauca</i> | * <i>Pinus coulteri</i> |
| * <i>Arctostaphylos pungens</i> | * <i>Prosopis juliflora</i> var. <i>glandulosa</i> |
| * <i>Ceanothus divaricatus</i> | <i>Prunus andersonii</i> |
| <i>Cupressus forbesii</i> | <i>Prunus fremontii</i> |
| * <i>Ephedra</i> spp. | <i>Pseudotsuga macrocarpa</i> |
| * <i>Fraxinus dipetala</i> | <i>Quercus palmeri</i> |
| <i>Juglans californica</i> | <i>Rhus laurina</i> |
| * <i>Lepidospartum squamatum</i> | |

range northward into central California in the Coast Ranges, the southern San Joaquin Valley, or the lower southern Sierra Nevada Mountains, but they are not characteristic in their northern extension. Only one of the above listed species now confined to southern California has been recorded in the deposits farther north: fragments of *Rhus* leaves in the Orinda flora are referable to *R. laurina*.

Eleven of the 30 living representatives of the Mount Eden flora are common to northern and southern California. The species marked by an

- | | |
|---------------------------------|------------------------------|
| <i>Ceanothus cuneatus</i> | * <i>Quercus agrifolia</i> |
| * <i>Cercocarpus betuloides</i> | * <i>Quercus chrysolepis</i> |
| <i>Equisetum</i> sp. | * <i>Salix lasiolepis</i> |
| <i>Pinus tuberculata</i> | * <i>Salix exigua</i> |
| * <i>Platanus racemosa</i> | <i>Typha angustifolia</i> |
| <i>Populus tremuloides</i> | |

asterisk represent modern correlatives of Mount Eden species recorded in the Pliocene floras of northern California. All of the others, with the possible exception of *Populus tremuloides*, would be expected in these deposits. The living equivalents common to the Mount Eden flora and the other Pliocene floras of California are wide-ranging species characteristic of much of California as a whole, and have been so since at least the Pliocene; this is evidenced by their occurrence throughout most of California in these deposits. As half of the flora is now characteristic of southern California and has not been recorded in deposits farther north, it seems apparent that southern California contained a distinct botanical element in the Pliocene which was then, as now, typical of that region. It may be concluded that the fundamental floristic segregation between northern and southern California had already been established in the Pliocene.

Dorf also notes¹ "in the Pliocene . . . a distribution of vegetation similar in aspect to that which now obtains in California." The differences between the Mount Eden flora and the other Pliocene floras in California (table 3) further suggest such a distribution. The species common to these various floras were characteristic of the California floral province, much as they are at present. It is significant that all Mount Eden species which do not occur in the Pliocene floras to the north find their greatest development in southern California, and that the species of the floras to the north which do not occur in southern California are primarily typical of the coastal and valley portions of northern and central California. This further suggests that barriers to migration, both climatic and topographic, were well established by Pliocene time in California. The dissimilarity between the Mount Eden flora and the other California Pliocene floras is due to geographic differences rather than to age discrepancy. The marked botanical changes which may be found in areas of diverse relief and climate, as in present-day California, can readily account for such floral segregation. Except for minor differences, southern California is evidently as floristically distinct from northern California today as it was in the Pliocene.

From the foregoing consideration of the vertebrate and plant evidence, the age of the Mount Eden flora may now be summarized. An absence of any typical Miocene species in the flora suggests a post-Miocene age. The correlation of the riparian and xeric elements of the Mount Eden flora with other California Pliocene floras substantiates a reference to the Pliocene, since the formations in which these floras occur are of definite Pliocene age. In addition, the species common to these assemblages are typical of the Pliocene. It seems evident that while a consideration of the flora from the standpoint of composition, distribution, and the physical conditions which it suggests, is in harmony with a reference to the Pliocene, the Mount Eden flora shows no great botanical similarity to any of the California Pliocene floras; the flora of southern California was floristically distinct by

¹ Carnegie Inst. Wash. Pub. No. 412, 57, 1930.

Pliocene time. It should be emphasized that the correlated species of these various floras were wide-spread in California during the Pliocene, and are of no close stratigraphic significance. Vertebrate evidence suggests a Middle Pliocene age for the Mount Eden beds, and the fossil plants are in accord with such a reference.

COMPARISON OF THE MOUNT EDEN FLORA WITH OTHER PLIOCENE FLORAS OF AMERICA AND ASIA

None of the other Pliocene floras of America shows a close similarity to the Mount Eden flora. The Esmeralda flora ¹ of western Nevada is of Lower Pliocene age ² and contains the following genera in common with the Mount Eden flora: *Populus*, *Quercus*, *Rhus*, *Salix*, *Sapindus*, and *Typha*. The *Sapindus* is probably similar to the Mount Eden species, for the living equivalent of *S. laciniifolius* was referred to as of a semiarid habitat, of which *S. drummondii* is typical. *Salix vacciniifolia* Knowlton was first referred to the modern *S. fluviatilis*, which resembles the Mount Eden *Salix* sp. Dorf; subsequently, Berry described the material as *Vaccinium*. The *Quercus* represents a scrub oak type but is referable to a different living species than the Mount Eden scrub oak. The *Populus* and *Rhus* show no relation to the Mount Eden species.

An *Arbutus* is apparently present in the Esmeralda flora, although it has been designated as *Chrysobalanus pollardiana* Knowlton. This species was referred to the living *C. icaco*, which is typical of coastal shores from southern Florida to the West Indies and Central America. Such a species would not be in accord ecologically with this semiarid flora. It is to be noted that the figured specimen shows a closer resemblance, in both shape and venation, to *Arbutus* than to *Chrysobalanus*, and is apparently related to the living *A. menziesii* of the Pacific Coast, rather than to the Mexican *A. xalapensis* to which the Mount Eden species was referred.

The Esmeralda flora is semiarid in aspect and lacustrine in origin; 6 genera in this assemblage represent hygrophilous plants. It is of interest that Chaney has noted a correlation between semiarid climates and the accumulation of plant remains in shallow lakes,³ for both the Esmeralda and the Mount Eden floras are in accord with this suggestion.

Several floras from the High Plains will now be compared with the Mount Eden flora, but their botanical relationships to this flora are even less apparent than are those of the California Pliocene floras.

A florule ⁴ from Brown County, Nebraska, is evidently transitional between the Miocene and Pliocene in age, and contains 5 genera: *Cyperacites*, *Fraginus*, *Platanus*, *Salix*, and *Typha*. The latter two, *Salix coalingsensis*

¹ Knowlton, U. S. Geol. Surv., 21st Ann. Rept., pt. 2, 216, 1900; Berry, U. S. Nat. Mus., Proc., vol. 72, art. 23, 1928.

² Stirton, Amer. Jour. Sci., vol. 32, 183, 1936.

³ Svenska Sällskapet för Antropologi och Geografi, Geografiska Annaler. Sven Hedin, 1935.

⁴ Chaney and Elias, Carnegie Inst. Wash. Pub. No. 476, 1936.

and *Typha lesquereuxi*, are represented in the Mount Eden flora. The small number of species in this Nebraska florule is in itself suggestive of a habitat unsuited for forested areas. Such trees as ash, willow, and sycamore are widely distributed along stream borders in semiarid regions where mesic forest types are absent. This assemblage is indicative of a more xeric type of vegetation than was generally accumulating in the Great Basin province during the latest Miocene, and is somewhat similar in aspect to the Esmeralda flora of western Nevada.

The Lower to Middle Pliocene flora of Beaver County, Oklahoma,¹ contains several genera in common with the Mount Eden flora, namely, *Fraxinus*, *Platanus*, *Typha*, *Salix*, *Sapindus*, and *Populus*. As above, *Typha* and *Salix* are similar to the Mount Eden species and the *Sapindus* was referred to the same modern equivalent, *S. drummondii*. However, the remaining genera in the Beaver County flora which are absent in the Mount Eden flora give the assemblage a different aspect. The living equivalents of *Diospyros*, *Acer*, *Gymnocladus*, *Hamamelis*, and *Bumelia*, in addition to the *Fraxinus*, *Populus*, and *Platanus*, now occur in eastern Oklahoma and represent broad river-bottom or flood-plain associations. *Cercidiphyllum* is an Asiatic element in the flora which now occurs in Japan, and is a relict occurrence of a former wide-spread Miocene species. The eastward restriction of this flood-plain association for a distance of nearly 100 miles in Oklahoma represents a reduction in rainfall of approximately 10 inches at the fossil locality since the early Pliocene.

The Middle Pliocene florule from Logan County, Kansas,² contains the following genera: *Celtis*, *Cyperacites*, *Populus*, *Salix*, *Typha*, and *Ulmus*. The willow, *Salix coalingsensis*, and *Typha lesquereuxi* are both present in the Mount Eden flora. The very paucity of species in this florule is suggestive of conditions unfavorable for wide-spread forest growth; the species are primarily riparian elements of semiarid areas, while the *Ulmus* is a xeric type. This flora is more similar in aspect to the Orinda and Etchegoin floras of central California than to the Mount Eden flora.

Boraginaceous nutlets, husks of various grasses, seeds of *Celtis*, and questionable remains of *Yucca* have been recorded in the Pliocene florules from Kansas and Nebraska.³ These assemblages represent an herbaceous vegetation of semiarid plains and prairies, and are indicative of a climate somewhat similar to that which exists in those areas today.

Plant remains associated with a vertebrate fauna in the Lower Pliocene Clarendon⁴ deposits of Texas include⁵ wood of *Fraxinus*, seeds of a palm, and the fruit of an *Arctostaphylos*. The latter material is referable to either *A. pungens* or *A. glauca*, both of which are represented in the Mount

¹ *Ibid.*, 1936.

² *Ibid.*, 1936.

³ Elias, Amer. Jour. Sci., vol. 29, 24-33, 1935.

⁴ Stirton, Amer. Jour. Sci., vol. 32, 1936.

⁵ Mason, oral communication, October, 1935.

Eden flora. It may be recalled that wood of a palm has been recorded from the Lower Pliocene Ricardo flora of the Mohave Desert. On the basis of such scanty material, it is difficult to draw any conclusions regarding the climatic conditions which prevailed in the Clarendon region during the Pliocene. The assemblage is suggestive of a warmer and drier climate than was present in the florules farther to the north in Oklahoma, Kansas, and Nebraska. This florule is similar to the Ricardo flora, in that both are probably referable to an origin in northern Mexico.

The Citronelle flora¹ of the Gulf States does not contain any species with which those of the Mount Eden flora can be compared. The difference between these floras is of the order of that between the present vegetation of the southeastern United States and that of southern California. A similarity to be noted between the Citronelle and the California Pliocene floras is that they are represented by living equivalent vegetation at no great distance from the areas in which the respective floras were collected. The Citronelle flora is typically a lowland, river-bank, estuarine association, with a few species indicative of drier habitats in adjacent areas; the living equivalent vegetation of this assemblage now occurs throughout the Gulf region.

As might be expected, the Pliocene florules of China² show no botanical similarity to the Mount Eden flora. A general restriction of forest areas and a semiarid aspect is to be noted in these Asiatic florules, and cooler temperatures were existent in these more northern localities.

While the Pliocene floras of California, the Great Basin, the High Plains, and China show but little botanical relationship, they suggest an aridity of climate which was evidently contemporaneous in these widely separated areas. All are corroborative of evidence indicating limited rainfall and a topography of high relief, which confined woody vegetation to lake borders, watercourses, well-watered valleys, and to cooler and moister slopes.

Pliocene floras are indicative of limited rainfall, extremes of temperature, and a topography of high relief which exerted a controlling influence on the distribution of vegetation. In addition, Pliocene floras exhibit conspicuous changes within limited areas and show marked floristic differentiation and geographic segregation. In direct contrast to these assemblages, Miocene floras are indicative of wide-spread forests and are suggestive of more uniform climatic and topographic conditions in the areas where plants were accumulating. While Pliocene floras are represented by equivalent living vegetation at no great distance from the fossil areas, Miocene assemblages are generally related to regions which are geographically remote from the fossil localities. This is a direct reflection of a greater age, since Miocene floras have been more altered in composition in response to widely changing physical conditions than have Pliocene floras. In addition, it is to be noted that all Pliocene species show closer resemblances to their modern equivalents than do Miocene species.

¹ Berry, U. S. Geol. Surv., Prof. Paper 98. 193. 1917.

² Chaney, Bull. Geol. Soc. China, vol. 12, no. 2, 1933; *ibid.*, vol. 14, no. 3, 1935; Svenska Sällskapet för Antropologi och Geografi, Geografiska Annaler, Sven Hedin, 1935.

SUMMARY

The Mount Eden flora, comprising 30 species, is of Middle Pliocene age. Twenty-six of the modern equivalents of the flora may now be found in southern California. Of the remainder, 2 species represent a *Pinus-Quercus* association, the digger pine forest, now growing north of the southern California province, and 2 others are Sonoran in present distribution. The fossil flora may be grouped into six distinct habitat associations representing a transect of mountain slopes adjacent to a depositional basin; the climate in this basin was arid. A savanna surrounded the basin, which was occupied by shallow lakes and marshes, and a desert-border element existed in lower exposed situations. Riparian and chaparral species were abundant and coniferous associations were present on the surrounding slopes.

On the basis of vertebrate evidence, wide-spread chaparral expansion did not take place before the Quaternary. Increasing aridity and rising temperatures in southern California, in addition to recurring fires, have apparently favored the development of this scrub formation. Chaparral has supplanted areas of desert-border species in the Mount Eden region, coniferous associations which formerly occupied lower slopes, and relict areas of digger pine and walnut in interior southern California. The northward movement of the digger pine forest from southern California seems to be primarily related to the rising winter temperatures in that area since the Pleistocene. The Sonoran element of the flora was apparently segregated from the California province in response to a shift from summers with some rainfall to a precipitation confined to the winter season.

An absence of resemblance to other Pliocene floras is occasioned by features of local distribution, rather than by age discrepancy. The flora of southern California was as distinct from that of northern California in the Middle Pliocene as it is today.

SYSTEMATIC DESCRIPTIONS

PHYLUM PTERIDOPHYTA

ORDER EQUISETALES

Family EQUISETACEÆ

Genus EQUISETUM Linné

Equisetum sp.

Among the many stem fragments in the Mount Eden flora, 2 petrified nodal portions are definitely assignable to this genus. The best specimen is 1.8 cm. long and 8 mm. wide, and exhibits approximately 28 ridges encircling the node.

Equisetum is commonly found about the edges of streams, lakes, or marshes, and is suggestive of an aquatic-border habitat. Abundant *Typha* remains are also indicative of shallow lakes or marshes in the Mount Eden basin, and the geologic evidence further corroborates their presence.

Collection—Univ. Calif. Mus. Pal., No. 957.

PHYLUM SPERMATOPHYTA

CLASS GYMNOSPERMÆ

ORDER CONIFERALES

Family PINACEÆ

Genus PINUS Linné

Pinus hazeni n. sp.

(Plate 2, fig. 4)

One well-worn cone with 16 exposed seeds, and 2 additional separate seeds, are definitely referable to this species. Although many other cones are present in the collection, most of them are too battered and broken to be definitely distinguished from *Pinus pieperi*.

Description—Cone asymmetrically obovate; tapering to an acute-oblique tip; 14 cm. long and 6 to 7 cm. wide; scales worn away in transport, exposing 16 seeds; seeds generally globose-obovate, with an acute-obtuse base and an asymmetrically acute tip; average, 1.1 cm. long and 6 mm. wide; vestiges of a ridge of scale attachment present along the edge of the seeds.

Discussion—Only two species of pine in western America have cones resembling those of the Mount Eden beds, namely, *Pinus coulteri* Don. and *P. sabiniana* Dougl. On the basis of fossil cone material alone, it is not possible to distinguish between these species. The seeds of these two pines, however, are easily recognized. Since the seeds of *Pinus hazeni* are globose, the fossil material is referred to *P. coulteri* rather than to *P. sabiniana*, in which the seeds are oblong and somewhat larger.

This is the first occurrence in the fossil record of a pine referable to *Pinus coulteri*. Its absence from other deposits may be due to the fact that it generally grew in situations rather remote from sites of deposition. The modern equivalent of *P. hazeni*, *P. coulteri*, is characteristic of drier slopes, ridges, and flats at middle elevations throughout southern California, where it occurs in the upper chaparral and the lower yellow pine forests; in more favorable localities it is often associated with big-cone spruce. Coulter pine is scattered northward to Mount Diablo on the inner Coast Ranges, and in its northern range commonly occurs on the upper borders of the digger pine forest; southward, it ranges into Baja California. Implications would favor the presence of *Pinus hazeni* above the digger pine forest on dry slopes surrounding the Mount Eden basin.

The species is named in honor of Mr. Guy Hazen, who has collected much of the material described in this paper.

Collection—Univ. Calif. Mus. Pal., Holotype, No. 958. Los Angeles Museum, Paratype, $\frac{1014}{719}$.

Pinus pieperi Dorf

(Plate 2, figs. 2, 3)

Pinus pieperi Dorf, Carnegie Inst. Wash. Pub. No. 412, 69-70, pl. 5, figs. 7-10, 1930.

Abundant remains in the Mount Eden flora make possible a definite determination of this species. The material, which comprises 2 complete and a number of fragmental cones, numerous seeds, and many cone scales, exhibits a wide range of variation comparable to that found in the modern

equivalent, *Pinus sabiniana* Dougl. There are, in addition, three cone stalks which may be referable to this species, or which may represent material of *P. hazeni*.

Pinus sabiniana usually forms open savanna and woodland associations throughout the foothills of the Great Valley of California and extends southward in the Coast Ranges into the Santa Ynez Mountains. The southernmost extension of the digger pine forest is to be found on the borders of Antelope Valley on the edge of the Mohave Desert. This species grows in typically hot dry valleys, and on arid foothills where the ground cracks and bakes during the summer and winters are cold. Digger pine is typically associated with xeric oaks and chaparral species. The abundance of *Pinus pieperi* in the flora is suggestive of a similar habitat of dry, baked, open slopes surrounding the Mount Eden basin.

Collection—Univ. Calif. Mus. Pal., Plesiotypes, Nos. 959, 960.

Pinus pretuberculata n. sp.

(Plate 3, figs. 3, 4)

Two cones are definitely referable to a closed-cone pine, and 4 additional battered cones probably belong to the same species.

Description—Distinctly obovate in shape; best-preserved cone is 8.4 cm. long, 5.5 cm. wide at the base and narrowing to 2.5 cm. near the apex, 3.6 cm. thick in its crushed plane; scales well preserved as spiral impressions, swollen on the lower side; in another cone a close packing of scales is apparent on one side which seems to have been attenuate.

Discussion—The material is undoubtedly a closed-cone pine and closely resembles *Pinus tuberculata* Gord. Of the California closed-cone pines, all but *P. tuberculata* are coastal in distribution. It is significant that the rest of the flora is also typically interior rather than maritime in aspect.

Pinus knowltoni Chaney¹ is probably referable to *P. tuberculata*, and has been recorded from a number of western Miocene floras. *Pinus tuberculata* has been recorded from the auriferous gravels near You Bet, California, and may be either Pliocene or Pleistocene in age.² The only definite Pleistocene occurrence of this species is from the Rancho La Brea deposits near Los Angeles.³ Although *Pinus linguiformis* Mason from Signal Hill, Los Angeles, is of Pleistocene age, it shows a tendency both to a *P. tuberculata* type and to a *P. masoni-muricata* complex.⁴

Pinus tuberculata is distributed from southern Oregon southward through California at elevations from 1000 to 5000 feet. It usually grows on dry, exposed south slopes and on poorer soils. The presence of *P. pretuberculata* in the flora is indicative of exposed slopes surrounding the Mount Eden basin in the Pliocene.

Collection—Univ. Calif. Mus. Pal., Plesiotype, No. 961. Los Angeles Museum, Cotypes, L. $\frac{1306}{1014}, \frac{1014}{696}, 688$.

¹ Walk. Mus. Contr., vol. 6, No. 5, 160, 1920.

² Mason, Carnegie Inst. Wash. Pub. No. 346, pt. 5, 148, 1927.

³ Frost, Univ. Calif. Pub. Bot., vol. 14, no. 3, 75, 1927.

⁴ Mason, Madroño, vol. 2, no. 6, 50, 1932.

Genus PSEUDOTSUGA Carr.

Pseudotsuga premacrocarpa n. sp.

(Plate 3, figs. 1, 2)

This species is abundantly represented by cones, many of which are crushed; the cone scales are usually well worn and appressed. Two broken concretions have exposed longitudinal sections of cones, in which seed cavities and bracts are discernible.

Description—Cones broad-oval to oblong; obtuse to rounded base and acute to obtuse tip; length 6.0 to 7.4 cm.; width 2.7 to 4.0 cm.; scales well preserved in only one specimen, the larger are 2 cm. broad, broadly curved in cross-section, and departing at 30° to 50° from the axis; thin bracts present in the longitudinal section of the cone; seed cavities 6 mm. long and 3 mm. wide, asymmetrically ovoid.

Discussion—*Pseudotsuga sonomensis* Dorf is referable to the living *P. taxifolia* Britt., from which *P. premacrocarpa* is clearly distinct. A remarkable similarity to the fossil species is found in the living *P. macrocarpa* Mayr. of southern California. Although Penhallow¹ reports *P. macrocarpa* from the Mad River of Humboldt County, California, Mason² has shown that the specimen is undoubtedly assignable to *P. taxifolia*. Seeds of *P. masoni* MacGinitie recorded from the Trout Creek, Austin-Tipton, and Upper Cedarville floras are likewise referable to *P. taxifolia* rather than to *P. macrocarpa*.

Pseudotsuga macrocarpa is abundant throughout southern California in cool canyons and on north slopes, and ranges northward into the San Rafael Mountains in Santa Barbara County, and southward into Baja California. In favorable areas, as on the north slope of San Bernardino Peak, big-cone spruce may form dense forests. In protected gulches it often extends into the lower chaparral as thin stringers and in small clumps. These isolated areas are relicts of a species which formerly was more widely distributed. Its range at lower altitudes has been greatly decreased by fire, following which the big-cone spruce does not sprout, and the invading chaparral is quickly stabilized. In view of the abundance of *Pseudotsuga* in the Mount Eden flora, it seems apparent that that species was then growing at lower elevations than its present living equivalent. The character of the Mount Eden sediments further corroborates this assumption, for they are of fine, rather than of coarse clastics; conglomeratic material is typically associated with plant material derived from upland areas.

Collection—Univ. Calif. Mus. Pal., Cotypes, Nos. 962, 963, 964. Los Angeles Museum, Cotypes, Nos. L. $\frac{1313}{6}$, $\frac{1014}{749}$.

Family CUPRESSACEÆ

Genus CUPRESSUS Linné

Cupressus preforbesii n. sp.

(Plate 2, fig. 1)

Two typical cypress cones are present in the collection, and both are crushed and flattened. The scales are too battered to afford any clue as to their external nature.

¹ Roy. Soc. Canada Trans., 2d ser., vol. 10, sec. 4, 70, 1904.

² Carnegie Inst. Wash. Pub. No. 346, pt. 5, 151, 1927.

Description—Asymmetrically oval shaped; one measures 1.8 cm. in length, 2.1 cm. in width, and 1.3 cm. in its flattened plane; the other is 2.4 cm. long, 2.5 cm. wide, and 1.5 cm. in its compressed plane.

Discussion—Although several *Cupressus* species have been recorded from the Pleistocene of California, only one occurrence has been noted in the Pliocene. Wood of a cypress was found in the Ricardo beds,¹ but reference to a living correlative was not possible because histological features were poorly preserved. Consequently, *C. nevadensis* Abrams, *C. forbesii* Jepson, and *C. arizonica* Greene were all suggested as living representatives.

Since the present taxonomic distinction among the 7 modern endemic cypress species of California is based on minor structural differences, reference to a modern equivalent can only be based on distribution and associate species. In its northernmost occurrence, on the north slope of Sierra Peak, *Cupressus forbesii* is associated with 60 per cent of the modern representatives of the Mount Eden flora; southward, in San Diego County and Baja California, many typical Mount Eden equivalents are also found among its associates. Of the other California species, *C. macrocarpa* Hartw., *C. goveniana* Gord., and *C. pygmæa* Sarg. are coastal in distribution; *C. nevadensis* Abrams is localized on Piute Mountain, Kern County; *C. macnabiana* Murr. is found far to the north, and *C. sargentii* Jepson is also typically northern, although an isolated locality occurs in the northern San Rafael Mountains in the south Coast Ranges. Evidence strongly points to a reference of the fossil material to *C. forbesii*, for many of its typical associates are represented by Mount Eden equivalents, and but few grow with the other cypress species. Furthermore, *C. forbesii* is characteristically an interior type, as are the other Mount Eden species, while the remaining *Cupressus* species are coastal or northern in distribution.

Collection—Univ. Calif. Mus. Pal., Cotypes, Nos. 965, 966.

ORDER GNETALES

Family GNETACEÆ

Genus EPHEDRA Linné

Ephedra sp.

A small concretion contains a carbonized stem fragment, which consists of a node and part of the adjoining internodes. Mr. Lyman H. Daugherty, who has kindly examined the material, states² that although some structural details are lacking, sufficient histological features are preserved to favor strongly a reference of the material to *Ephedra*. The fragment is 3.4 cm. long and 2 mm. wide and closely resembles the apical portion of an *Ephedra* stem.

The additional presence of *Prosopis* and *Prunus* spp. in the flora is fully in accord with a reference to this genus, since *Ephedra* is typically associated with these shrubs throughout their desert-border range. *Ephedra* also occurs at the mouth of Whitewater Canyon on the edge of the Colorado Desert, where some 13 Mount Eden equivalent species now grow. A similar occurrence on dry, exposed lower slopes and flats surrounding the depositional basin is suggested for its Mount Eden habitat.

¹ Webber, Carnegie Inst. Wash. Pub. No. 412, pt. 2, 122, pl. 2, figs. 1-3, 1933.

² Written communication, February, 15, 1936.

There are only two other American Tertiary records of this genus. Pollen of *Ephedra eocenipites* Wodehouse¹ is abundant in the Green River shales, but relationship to the Mount Eden species is questionable. A stem fragment of *Ephedra miocenica* Wodehouse² from the Florissant has been referred to *E. nevadensis*, a common species on the Mohave and Colorado Deserts in California. It is possible that the Mount Eden species is also referable to *E. nevadensis*, although several other species occur on the California deserts.

Collection—Univ. Calif. Mus. Pal., No. 1007.

CLASS ANGIOSPERMÆ

Subclass MONOCOTYLEDONÆ

ORDER PANDANALES

Family TYPHACEÆ

Genus TYPHA Linné

Typha lesquereuxi Cockerell

Typha lesquereuxi Cockerell, Bull. Torrey Bot. Club, vol. 33, 307, 1906.

Many fragmentary remains of *Typha* were noted at the several localities. Numerous apices,³ impressions of a subbasal fragment, and a middle leaf portion are present in the collection.

Since diagnostic characters on the basis of impressions only are lacking for the determination of species of this genus, the material has been referred to *Typha lesquereuxi*, a wide-ranging Tertiary aquatic-border element of no stratigraphic significance. The material shows a relationship closer to *T. angustifolia* L. than to *T. latifolia* L., on the basis of the vertical ridging of the stalks, which in *T. angustifolia* and in the fossil material is much more distinct and definite than in *T. latifolia*.

Typha angustifolia is a typical lake- and marsh-border element, and is also present in the meandering and marshy portions of the Santa Ana River at the base of Sierra Peak with associates of poplars, willows, sycamores, walnuts, oaks, *Equisetum*, and *Lepidospartum*.

Collection—Univ. Calif. Mus. Pal., No. 967.

Subclass DICOTYLEDONÆ

ORDER SALICALES

Family SALICACEÆ

Genus POPULUS Linné

Populus pliotremuloides n. sp.

(Plate 4, figs. 1, 2, 3)

Description—Leaves ovate; tip acute, base subcordate or truncate; largest leaf 3.5 cm. long and 3.3 cm. wide, a smaller one measures 2.9 cm. wide and 2.7 cm. long; petiole 1.7 cm. long, slender; midrib medium-textured, straight below and displaced by the departing secondaries above; 6 secondaries, the lower pair opposite and those above alternate, departing at angles of 40° to 50°, forking near the margin to join the one above, venation obscure along

¹ Wodehouse, Bull. Torrey Bot. Club, vol. 60, 495, 1933.

² Wodehouse, Torrey, vol. 34, no. 1, 1, 1934.

³ These were first referred to *Graminites*; see Axelrod, Amer. Mus. Novitates, No. 729, 1934.

the margin; 4 to 6 subparallel tertiaries diverging at 50° from the abaxial side of the lower secondaries, curving slightly upward; other tertiary venation indistinct, though evidently irregularly percurrent; margin crenate; texture firm.

Discussion—A diligent search was made for a plant resembling this species among the modern plant assemblages in southern California, but none was found to resemble it. In herbarium studies, however, a close resemblance was noted to *Populus tremuloides* Michx., but since this species is typically found in the higher mountains of western America, it would hardly be expected in a flora accumulating in an arid basin. Dr. H. L. Mason suggested that the fossil species might be referable to this species, since he noted this aspen along alluvial fans at the base of the Ruby Mountains in a semiarid habitat in Nevada. This same species was observed by Condit growing under similar conditions in the Roberts Mountains in Nevada. A meadow in a cold canyon supported a small grove of *P. tremuloides*, and a semiarid habitat prevailed in the adjacent area. In addition, Goldman¹ has reported aspen at lower elevations in Baja California with a surrounding arid habitat; Sudworth² has also recorded aspen in the arid portions of eastern Oregon and California. Evidently such a distribution may be found along canyons where there is a downward flow of cold water and air, establishing at lower levels requisite conditions for establishment; such irregularities in distribution are not uncommon.

Several described *Populus* species have been referred to a *P. tremuloides* type, but their relations to the Mount Eden species are ecologically obscure. Among these may be mentioned *P. neotremuloides* Knowlton,³ *P. microtremuloides* Knowlton,⁴ *P. glandulifera* Heer,⁵ and *P. lindgreni* Knowlton.⁶ Although several of these species, especially *P. lindgreni*, do resemble *P. tremuloides*, and may well represent the fossil form of this species, the writer believes that the Mount Eden species is distinct in its ecologic implications.

Although most Mount Eden species are of scanty occurrence, it is significant that this species is represented by 6 complete leaves. Its abundance in the flora is suggestive of adjacent highlands with deep cool canyons supporting *Populus plicatremuloides* which approached close to the Mount Eden basin.

Collection—Univ. Calif. Mus. Pal., Cotypes, Nos. 968, 969, 975.

Genus SALIX Linné

Salix coaligensis Dorf

(Plate 4, fig. 8)

Salix coaligensis Dorf. Carnegie Inst. Wash. Pub. No. 412, 78-79, pl. 7, figs. 5-7; pl. 8, figs. 1, 2, 1930.

Six complete and nearly complete leaves, as well as a number of fragments, are represented in the collection. As in the Pliocene floras to the north, this species is one of the most abundant elements of the Mount Eden flora. Although, as emphasized by Dorf, close resemblances may be noted to *Salix*

¹ Contr. U. S. Nat. Herb., vol. 16, pt. 13, 319, 1913.

² *Forest Trees of the Pacific Slope*, 243, 1908.

³ U. S. Geol. Surv., Prof. Paper 101, 296, pl. 66, fig. 2, 1918.

⁴ U. S. Nat. Mus., Proc., vol. 51, 261, pl. 19, fig. 2, 1916.

⁵ U. S. Geol. Surv., Mon. 32, pt. 2, pl. 84, fig. 1, 694, 1899.

⁶ U. S. Geol. Surv., 18th Ann. Rept., pt. 3, 725, pl. 100, fig. 5, 1898.

lasiandra Benth. and *S. laevigata* Bebb, the leaves of this species show a degree of variability comparable to that exhibited by *S. lasiolepis* Benth., which is therefore considered as the nearest modern equivalent.

Salix lasiolepis is the most abundant willow throughout California at lower elevations. In southern California it is commonly associated with sycamores, alders, walnuts, poplars, ash, and oaks. Its abundance in the flora is indicative of a well-developed riparian element.

Collection—Univ. Calif. Mus. Pal., Plesiotype, No. 978.

***Salix* sp. Dorf**

(Plate 4, fig. 7)

Salix sp. Dorf. Carnegie Inst. Wash. Pub. No. 412. 79-80, pl. 8, fig. 3. 1930.

Long, narrow leaves of willow have been found in the Santa Clara and Orinda floras, but abundant material is wanting. None of the leaves studied by Dorf were sufficiently complete to warrant a description, but they were clearly recognized as being related to the living *Salix exigua* Nutt. One complete leaf in the Mount Eden flora is also referable to *S. exigua*. Although it is smaller than those collected by Dorf, this specimen readily falls within the range of variation exhibited by *S. exigua*.

The leaf is narrow and slender, the very tip is missing, though evidently acute; gradually narrowing to a cuneate base; 1.3 cm. long and 2 mm. wide; petiole 3 mm. long; midrib straight and heavy; secondaries and tertiaries absent; margin entire; texture medium.

The Mount Eden species, as well as the material of the Orinda and Santa Clara floras, seems definitely related to *Salix exigua* Nutt., a wide-ranging species from British Columbia southward to southern California, and eastward to Nebraska and Kansas. It is noteworthy that a resemblance may also be found with *S. hindsiana* Benth. of southern California. *Salix vac-cinifolia* Knowlton of the Esmeralda flora¹ was referred to the living *S. fluviatilis*,² but Berry has shown that the leaves are referable to *Vaccinium*.³

Collection—Univ. Calif. Mus. Pal., Plesiotype, No. 970.

ORDER JUGLANDALES

Family JUGLANDACEÆ

Genus JUGLANS Linné

***Juglans beaumontii* n. sp.**

(Plate 4, figs. 11, 12)

This species is represented by a number of fruits, some of which are crushed, and the apical portion of a leaflet.

Description—Leaflet oblong lanceolate; acute apex and base absent; 4.5 cm. long and 1.8 cm. wide; midrib straight and medium-textured; 12 secondaries arising alternately and departing at 40°, 4 mm. apart, some with sub-camptodrome tendencies, forking near the margin; occasional intersecondaries, indistinct; tertiaries not preserved; margin entire; texture firm. The fruits are deformed through crushing and transportation; broad-ovoid; size in larger specimens 2.3 cm. in diameter to 1.7 to 1.9 cm. in a vertical plane;

¹ U. S. Geol. Surv., 21st Ann. Rept., pt. 2, 212, pl. 30, figs. 8, 20, 1901.

² Formerly designated as *Salix fluviatilis exigua* (Nutt.) Sargent.

³ U. S. Nat. Mus., Proc., vol. 72, art. 23, 14, 1928.

5-locular, with 4 or 5 heavy vertical ridges of 2 mm. width on each locule; smaller specimens measure 1.4 cm. in an equatorial plane and 1.5 cm. vertically, occasionally deeply grooved.

Discussion—It is possible that the fruits in the flora may be related to two living species, *Juglans californica* Wats. and *J. rupprestris* Engelm. The majority of the walnuts in the flora are undoubtedly referable to the former species, but one of the smaller fruits (Plate 4, fig. 11) is almost identical with those of *J. rupprestris*. The grooves on the fruits of this species are much deeper than on those of *J. californica*, and the walnuts are generally somewhat smaller. However, since the size variation in *J. californica* may include that of *J. rupprestris* and since only one fruit is in the collection, two species were not recognized. Should further collections verify its presence in the flora, *J. rupprestris* would represent either a riparian or a desert-border element. This species occurs throughout the Southwest along streams and on alluvial fans from Arizona to Texas and southward into Sonora. Among its associates in this area are *Prosopis*, *Sapindus*, *Ephedra*, *Platanus*, *Salix*, and *Populus*.

Juglans californica is endemic to southern California and is abundant throughout the coastal region, where it reaches optimum development under an ameliorating oceanic influence. Several areas of this species in interior southern California are confined to streams in deep cool canyons, and appear to represent relict occurrences of a former widely developed association. None of the many Tertiary *Juglans* species show any relationships to this walnut.

Collection—Los Angeles Museum, Cotypes, Nos. L. $\frac{1313}{103}$, L. $\frac{1313}{127}$, $\frac{1014}{1}$.
Univ. Calif. Mus. Pal., Cotypes, Nos. 971, 972.

ORDER FAGALES

Family FAGACEÆ

Genus QUERCUS Linné

Quercus lakevillensis Dorf

Quercus lakevillensis Dorf, Carnegie Inst. Wash. Pub. No. 412, 82-84, pl. 8, figs. 4, 5, 1930.

Leaves of this species were at first believed to be abundant in the Mount Eden flora; however, further study has shown that most of these resemble variant leaf forms of the modern *Quercus palmeri* Engelm., rather than *Q. agrifolia* Née, the living equivalent of *Q. lakevillensis*. *Q. palmeri* differs from *Q. agrifolia* in the following manner: its secondaries depart at smaller angles from the midrib; in the dentate forms the lower secondaries are commonly recurved toward the base; the secondaries are not conspicuously branched; the texture is much coarser and is usually crisped; and there are differences in detail of tertiary venation. Only one complete leaf and a few fragments seem referable to *Q. lakevillensis*.

Several acorn impressions may be referred to *Quercus lakevillensis*, at least they are not comparable to *Q. palmeri* or to the living equivalents of the other two oaks in the Mount Eden flora, namely, *Q. orindensis* and *Q. chrysolepis*.

Quercus agrifolia is found through the Coast Ranges and southward into Baja California. It is more mesic in its requirements than *Q. douglasii* (Q.

orindensis) or *Q. palmeri* (*Q. pliopalmeri*), and typically forms savanna and woodland associations throughout its range; southward, it is commonly displaced by chaparral following fire.

Collection—Univ. Calif. Mus. Pal., Plesiotype, No. 973.

Quercus hannibali Dorf

(Plate 5, fig. 6)

Quercus hannibali Dorf, Carnegie Inst. Wash. Pub. No. 412, 86-88, pl. 8, figs. 8-11, 1930.

Several entire lanceolate-ovate leaves are indistinguishable from the living *Quercus chrysolepis* Liebm., to which Dorf referred the species. This is an oak widely distributed throughout California, and in southern California it is abundant at middle elevations associated with *Pseudotsuga macrocarpa*, *Pinus coulteri*, and the upper chaparral element.

Variation in the leaf shape of the living species is extreme; entire lanceolate and deeply serrated suborbicular leaves may be found on the same twigs. Although a number of serrate to pungent-dentate oval and suborbicular leaves occur in the flora, they have been recognized as a new species, *Quercus pliopalmeri*, which is referable to *Q. palmeri* Engelm. This species differs from *Q. chrysolepis* in its crisped texture and the character of the secondaries. In *Q. chrysolepis* the secondaries are parallel, while in *Q. palmeri* they depart at low angles near the base and at high angles near the apex. Although *Q. palmeri* may have entire lanceolate-ovate leaves,¹ such an expression is not typical of the species; these leaves are not distinguishable from those of *Q. chrysolepis*. The presence of *Pseudotsuga premacrocarpa* and *Pinus hazeni* in the flora further substantiates the existence of *Q. hannibali* in the Mount Eden area, for it is a typical associate of the living equivalents of these conifers today.

Collection—Univ. Calif. Mus. Pal., Plesiotypes, Nos. 974, 976.

Quercus orindensis Dorf

(Plate 5, fig. 7)

Quercus orindensis Dorf, Carnegie Inst. Wash. Pub. No. 412, 89-90, pl. 9, figs. 6-9, 1930.

Two nearly complete leaves show excellent details of venation, and with 2 additional impressions aptly illustrate the leaf variation to be found in this species. The obovate-lanceolate leaves with entire-lobate margins may, without question, be referred to the modern *Quercus douglasii* H. & A., for no outstanding differences between leaves of this species and the fossil are to be noted.

Quercus douglasii is characteristic of the dry foothills surrounding the Great Valley of California, and finds its southern limits with *Pinus sabiniana* about Antelope Valley. It is one of the most xeric of California oaks, and is a typical component of the digger pine forest, although it usually extends well below the forest into the drier foothills. *Quercus orindensis* is further suggestive of dry open slopes bordering the Mount Eden basin.

Collection—Univ. Calif. Mus. Pal., Plesiotypes, Nos. 977, 979.

¹ Trelease, Mem. Nat. Acad. Sci., vol. 20, pls. 213-214, 1924.

Quercus pliopalmeri n. sp.

(Plate 5, figs. 1, 2, 3)

This species is particularly abundant in the flora, and exhibits considerable variation in size and shape.

Description—Ovate to suborbicular in shape; tips acuminate or apiculate; base obtuse to subcordate; larger leaves 2.8 cm. long and 4.0 cm. wide, smaller ones are 2.0 cm. long and 1.5 cm. in width; midrib straight or recurved and very stout; petiole short, 2 to 3 mm. long; 5 to 7 alternate secondaries, always recurved in the pungent-dentate leaves, otherwise straight, departing at 20° to 50°, occasionally forking near the margin, recurving toward the base in the suborbicular leaves; irregular tertiary venation; margin serrate or pungent-dentate; texture both coriaceous and crisped.

Discussion—The task of differentiating between the leaf forms of several of the western xeric oaks is an exceedingly difficult one. Although variations in *Quercus agrifolia* Née and *Q. wislizenii* A. de C. approach the fossil species, the serrate leaves of *Q. chrysolepis* are often inseparable from those of the modern equivalent of this species, *Q. palmeri*. The leaves of this latter species are usually of heavier texture, resulting in a curling and crisping which is more extreme than in *Q. chrysolepis*. Furthermore, while the secondaries of *Q. chrysolepis* are nearly parallel, the lower pairs in *Q. palmeri* depart at very low angles and are commonly recurved, while the upper ones depart at 40° to 50°. In addition, *Q. chrysolepis* usually has from 2 to 3 more pairs of secondaries than *Q. palmeri*.

Exclusive of those serrate forms resembling *Quercus hannibali*, only one other fossil oak shows any relationship to this species. *Q. turneri* Knowlton,¹ which represents a shrubby form recorded from the Esmeralda flora, was referred to the living *Q. turbinella* Greene.² The figured specimen differs from *Q. pliopalmeri* in the secondaries which weaken and waver near the margin, and in the character of the dentation.

Quercus palmeri ranges through the San Jacinto Mountains and southward into Baja California. It is a common chaparral element, although it is not widely developed anywhere; among its associates are species of *Arctostaphylos*, *Ceanothus*, and *Cercocarpus*. Throughout its range *Q. palmeri* is often found bordering desert regions. As a dominant element of the flora, it was probably abundant on the lower slopes about the Mount Eden basin.

Collection—Univ. Calif. Mus. Pal., Cotypes, Nos. 980, 981, 982, 988.

ORDER ROSALES

Family PLATANACEÆ

Genus PLATANUS Linné

Platanus paucidentata Dorf

(Plate 5, figs. 4, 5)

Platanus paucidentata Dorf, Carnegie Inst. Wash. Pub. No. 412, 94-96, pl. 10, figs. 4, 9; pl. 11, fig. 1; pl. 12, fig. 1, 1930.

The abundant well-preserved remains of this species constitute one of the dominant elements of the flora. Several nearly complete leaves and a number of fragments are represented in the collection.

¹ Knowlton, U. S. Geol. Surv., 21st Ann. Rept., pt. 2, 216, pl. 30, fig. 21, 1901.

² *Quercus dumosa turbinella* Jepson.

The material closely resembles two living species, *Platanus racemosa* Nutt. of central and southern California and *P. wrightii* S. Wats. of Arizona, New Mexico, and Sonora. It is possible that the Mount Eden sycamore, *P. paucidentata*, may be involved in the problem of speciation as related to aridity. It is significant that in southern California and on the borders of the Colorado and Mohave Deserts, the leaves of *P. racemosa* are often indistinguishable from those of *P. wrightii*. In its southern range the leaves of *P. racemosa* are commonly cordate and with deep attenuated lobes, as are those of *P. wrightii*. In details of shape, size, margin, and venation, the leaves of these two species are practically identical. Northward and in more mesic localities, however, the leaves of *P. racemosa* typically have truncate and cuneate bases and shallow lobes.

A somewhat similar implication may be noted in Dorf's Pliocene floras.¹ At Coalinga, the southernmost interior locality, *Platanus* leaves have deep attenuated lobes like those of the Mount Eden flora. The Etchegoin florule is the most xeric of those described by Dorf, and contains *Quercus orindensis*, *Garrya*, and a well-developed riparian element. The association indicates conditions comparable to those of the semiarid slopes of the inner Coast Ranges bordering the Great Valley of California. However, in the Pliocene floras farther north *Platanus* has shallow lobes and truncate or cuneate bases. In all cases, the associate species are definitely more mesic in aspect than the florule from Coalinga. Similarly, in more mesic localities today the leaves of *Platanus* have shallow lobes and truncate or cuneate bases, rather than deep attenuated lobes and cordate bases such as are found on the trees growing along the edges of the deserts or in arid regions. Assuming *Platanus paucidentata*, the Pliocene equivalent of *P. racemosa*, to have been wide-spread in the Southwest in the Pliocene, as it was in California, it seems probable that *P. wrightii* was differentiated from that species in response to increasing aridity throughout the Southwest.

Platanus wrightii is a typical riparian element in the mountains of the Southwest. At lower altitudes it is commonly associated with species of *Juglans*, *Ephedra*, *Prosopis*, *Populus*, and *Salix*. *Platanus racemosa* is a common stream-bank species throughout southern California at lower elevations and may grow with willows, oaks, alders, ash, walnuts, and poplars. *Platanus paucidentata*, the Pliocene equivalent of *P. racemosa*, was a dominant element in many of the California Pliocene floras farther north. Included among its associates were willows, ash, alders, and poplars. The wide-spread occurrence of this sycamore in the Pliocene of California is indicative of its forming a constituent part of the California flora of that period, much as it does at present in the more arid portions of California.

Collection—Univ. Calif. Mus. Pal., Plesiotypes, Nos. 983, 984, 986.

Family ROSACEÆ

Genus CERCOCARPUS H. B. K.

Cercocarpus cuneatus Dorf

(Plate 4, fig. 4)

Cercocarpus cuneatus Dorf, Carnegie Inst. Wash. Pub. No. 412, 98-99, pl. 12, fig. 3, 1930.

One nearly complete leaf and 2 fragments constitute this record in the Mount Eden flora. These impressions strikingly resemble the modern *Cer-*

¹ Dorf, Carnegie Inst. Wash. Pub. No. 412, 1930.

cocarpus betuloides Nutt., to which Dorf referred the fossil form. It is a characteristic chaparral species throughout southern California, and is widely distributed from the Rocky Mountains to Oregon and southward into Baja California. In interior southern California, this species is best developed on north slopes at middle elevations. On the desert slopes in southern California, mountain mahogany may extend well below the pinyon belt.

Collection—Univ. Calif. Mus. Pal., Plesiotype, No. 987.

Genus PRUNUS B. & H.

***Prunus preandersonii* n. sp.**

(Plate 4, figs. 9, 10)

Three well-preserved seeds are in the collection and all may be definitely referred to the living *Prunus andersonii* Gray, since no appreciable difference exists between the fossil and modern species.

Description—Seeds globose, sub-oblique; tips acuminate, with a broadly rounded base; largest seed measures 1.3 cm. in width, 1.8 cm. in length, a smaller one is 1.2 cm. long and 9 mm. wide. A distinct ridge completely encircles the seed in the plane of its longest axis. The seeds are also somewhat flattened in this plane, as are those of its modern representative.

Discussion—*Prunus andersonii* is not an uncommon shrub on the eastern slopes of the San Jacinto, San Bernardino, and Sierra Nevada Mountains. Southward it is found on the edges of the Colorado and Mohave Deserts associated with *Prosopis*, *Ephedra*, and *Lepidospartum*.

None of the many described Tertiary species of *Prunus* are in any manner comparable to this species.

Collection—Los Angeles Museum, Cotypes, Nos. L. $\frac{1313}{94}$, L. $\frac{1313}{100}$, L. $\frac{1313}{112}$.

***Prunus fremontii* n. sp.**

(Plate 4, figs. 5, 6)

The following description is based on 4 of the best seeds in the collection; several others are somewhat crushed and broken.

Description—Globose and elliptic-ovoid in shape; with a broadly rounded base and apex; 2 to 3 longitudinal ridges on one side; 8 mm. to 1.0 cm. long and 7 mm. in diameter; several of the seeds are somewhat larger (2 mm.) than those of its modern equivalent, *Prunus fremontii* Wats.

Discussion—None of the many Tertiary *Prunus* species seem related to this species. *Prunus fremontii* is a typical desert-border shrub and occurs in the mountain ranges in and bordering the Colorado Desert, and ranges southward into Baja California. At the mouth of Whitewater Canyon, on the edge of the Colorado Desert, it was found in association with *Arctostaphylos glauca*, *Cercocarpus betuloides*, *Ephedra* spp., *Lepidospartum squamatum*, *Platanus racemosa*, *Salix exigua*, and *S. lasiolepis*; farther up the canyon, *Ceanothus divaricatus*, *Quercus chrysolepis*, *Pseudotsuga macrocarpa*, and *Pinus coulteri* were also noted. All of these species are represented in the Mount Eden flora by closely comparable fossil equivalents.

Collection—Los Angeles Museum, Cotypes, Nos. $\frac{1014}{822}$, $\frac{1014}{909}$, $\frac{1014}{912}$.

Family LEGUMINOSÆ

Genus PROSOPIS Linné

Prosopis pliocenica n. sp.

(Plate 6, figs. 2, 3)

Two complete leaflets and a fragment seem referable to this genus, and as far as known this is the first record of this genus in the fossil record.

Description—One leaflet oblong, the other slightly obovate in shape; base and apex obtuse; petiole none, evidently sessile; 1 cm. long and 4 mm. wide; midrib stout; 3 or 4 obscure alternate secondaries, diverging at 50°; tertiary venation absent; margin entire; subcoriaceous texture.

Discussion—*Prosopis* is typical of desert bottomlands throughout the Southwest. It occurs in the upper San Joaquin Valley in central California, and is occasional in interior southern California, where it grows in a Lower Sonoran habitat. On the Colorado Desert it has been noted in association with *Prunus andersonii* and *P. fremontii*, *Ephedra* spp., and *Lepidospartum squamatum*. Eastward, in Arizona, it may occur with *Sapindus drummondii*; all of these species are represented by fossil equivalents in the Mount Eden flora.

Collection—Univ. Calif. Mus. Pal., Cotypes, Nos. 989, 990, 991.

ORDER ERICALES

Family ERICACEÆ

Genus ARBUTUS Linné

Arbutus sp.

(Plate 6, fig. 1)

One large leaf, showing excellent details of venation, is quite distinct from any of the other leaves in the flora.

Lanceolate in shape; with an acute apex and obtuse base; 8.9 cm. long and 3.2 cm. wide; 7 mm. of a heavy stout petiole present; midrib heavy, straight, extending to the apex; 15 long alternate secondaries, with several obscured in the upper portion, departing at 40° to 45° with camptodrome tendencies; basal secondaries follow the margin to the upper pair, to which they connect by nervilles; several intersecondaries present; tertiary venation irregular in the broader areas, or irregular-percurrent on narrowing; finely serrate margin; texture coriaceous.

Arbutus matthesii Chaney¹ and *A. traini* MacGinitie² are both referable to *A. menziesii* Pursh. of the Pacific Coast, and are distinct from this species, which resembles the living *A. xalapensis* H. B. K. of Mexico. Standley³ recognizes some 10 described species of *Arbutus* as being variants of *A. xalapensis*. Northward, it includes such types as *A. petiolaris*, *A. prunifolia*, and *A. mollis*, which are entire-margined and much smaller than the Mount Eden species. In western Texas madrone is associated with *Cercocarpus*, *Cercis*, *Garrya*, *Agave*, *Yucca*, pinyon pine, juniper, and xeric oaks.⁴ In the Mexican Plateau, however, it is found with *Carya*, *Bauhinia*, black and

¹ Chaney, Carnegie Inst. Wash. Pub. No. 346, 131, pl. 20, figs. 1, 3, 4, 1927.

² MacGinitie, Carnegie Inst. Wash. Pub. No. 416, 64-66, pl. 13, figs. 1, 2; pl. 12, fig. 3, 1933; LaMotte, Carnegie Inst. Wash. Pub. No. 455, 1936.

³ Contr. U. S. Nat. Herb., vol. 23, pt. 4, 1100, 1924.

⁴ U. S. Dept. Agric., Biol. Surv., North American Fauna No. 25, 1905.

chestnut oak, *Juglans*, *Smilax*, *Vitis*, *Abies*, and *Alnus*.¹ This latter association grows at higher elevations and is indicative of greater rainfall and less extremes of temperature than the association to the north. It is significant that the Mount Eden madrone resembles these more mesic latter types. It may be suggested that the Mount Eden species was an expression of a moist upland habitat, rather than one of semiaridity.

Collection—Univ. Calif. Mus. Pal., No. 992.

Genus ARCTOSTAPHYLOS Adans.

Arctostaphylos preglaucula n. sp.

(Plate 6, figs. 8, 9)

Description—Asymmetrical leaf broadly ovate in shape; apex obtuse; base and petiole absent; 3.3 cm. long and 1.5 cm. wide; midrib stout and recurved; 8 or 9 subopposite secondaries rather indistinct, departing at 30° to 40° and curving upward at the margins to 50° to 60°; entire-margined; tertiaries absent; coriaceous textured. Two seed fragments, each representing half a solid stone, globose; 1.1 cm. wide and 1.0 cm. long, and 8 mm. long and 8 mm. wide.

Discussion—On the basis of foliar material alone, it was not possible to refer this species to any one modern equivalent, since resemblances to both *Arctostaphylos glauca* Lindl. and *A. glandulosa* Eastw. are apparent. Both are the most widely distributed and best-developed species of the genus in southern California. However, the fruits of the two species are sufficiently distinct to afford a determination. The nutlets of *A. glauca* are fused into a hard stone, while those of *A. glandulosa* are separate. The seed fragments definitely resemble those of *A. glauca*, and on this basis the leaf is also assigned to the same species, although it is possible that both species are represented—one by seed and the other by foliar material.

Seeds of *Arctostaphylos glauca* have been recorded from the Pleistocene of California and have been referred to the modern species.² Material from the Pliocene of Texas may be referable to this species, at least the seed resembles *A. glauca* in that the nutlets are fused.³ Hannibal has recorded *Arctostaphylos* leaves from the Pliocene Santa Clara flora, near Portola, California, but they were referred to the modern *A. manzanita*.⁴ Two *Arctostaphylos* leaves from the Latah⁵ show no resemblance to this species.

Arctostaphylos glauca is an abundant chaparral element throughout southern California, and ranges northward in the Coast Ranges. It is commonly associated with species of *Ceanothus*, *Cercocarpus*, *Rhus*, *Quercus*, and *Frazinus* which have representatives in the Mount Eden flora.

Collection—Univ. Calif. Mus. Pal., Cotypes, Nos. 997, 998, 999.

Arctostaphylos prepungens n. sp.

(Plate 6, figs. 10, 11)

This species is represented by 2 complete leaves and a seed. Both leaves are closely comparable to those of the modern *Arctostaphylos pungens* H. B. K., and the seed is referable to the same species.

¹ Chaney, oral communication, March, 1936.

² Chaney and Mason, Carnegie Inst. Wash. Pub. No. 415, 64, 1930.

³ Mason, oral communication, October 14, 1935.

⁴ Bull. Torrey Bot. Club, vol. 38, 339, pl. 15, fig. 5, 1911.

⁵ Berry, U. S. Geol. Surv. Prof. Paper 154, 261-262, pl. 59, fig. 4; pl. 64, fig. 6, 1929.

Description—Leaves ovate or obovate; narrowing above to an acute or subobtuse apex; base obtuse; larger leaf measures 2.1 cm. long and 1.0 cm. wide, smaller one is 1.5 cm. long and 9 mm. wide; petiole slender, 2 mm. long in the smaller leaf; venation indistinct, with 4 pairs of alternate secondaries diverging at 60° to 70°; tertiary venation absent; margin entire; coriaceous texture. Seed flattened-globose, composed of 5 or 6 nutlets; 8 mm. in diameter and 5 mm. in a vertical plane.

Discussion—An *Arctostaphylos* seed from the Lower Pliocene of Texas, near Clarendon, may be assignable to this species, although it also resembles *A. glauca*.¹ In general shape, *A. elliptica* Knowlton² is somewhat like the Mount Eden material, but the leaves are nearly twice as large and the venation is quite different. *A. elliptica* was believed referable to the wide-ranging north temperate *A. uva-ursi*. The *Arctostaphylos* recorded by Hannibal³ and Berry⁴ show no relation to this species.

Arctostaphylos pungens is a common species in the chaparral of southern California at middle elevations, but is not as widely developed as *A. glauca*. *A. pungens* may grow at lower altitudes in San Diego and southern Riverside Counties.

Collection—Univ. Calif. Mus. Pal., Cotypes, Nos. 993, 994, 995, 996.

ORDER RHAMNALES

Family RHAMNACEÆ

Genus CEANOTHUS Linné

Ceanothus edensis n. sp.

(Plate 6, fig. 4)

Two complete leaves and a fragment are diagnostic enough in all of their essential features to justify description as a new species.

Description—Oval-ovate in shape; broadly rounded and subcordate at the base; apex obtuse; larger leaf 2.1 cm. long and 2.1 cm. wide, smaller one is 1.5 cm. long and 1.0 cm. in width; petiole absent, but apparently short; venation 3-nerved, midrib straight, stout; the lower 2 opposite secondaries depart from the base of the midrib at 45°; 3 other obscure subopposite secondaries depart from the midrib at 50°; tertiaries absent; margin serrulate above and entire below; texture subcoriaceous.

Discussion—*Ceanothus eriensis* Knowlton,⁵ which was referred to *C. americanus* L., seems to antedate a tri-nerved type, but shows no relation to this species. The several other described Tertiary *Ceanothus* species show no affinities to the Mount Eden species, which is referable to the living *C. divaricatus* Nutt. *C. divaricatus* ranges from Baja California northward throughout the southern California chaparral, and is scattered in the central Coast Ranges and lower central Sierras. Among its associates are species of *Arctostaphylos*, *Ceanothus*, *Rhus*, and *Fraxinus*.

Collection—Univ. Calif. Mus. Pal., Cotypes, Nos. 1000, 1001.

¹ Mason, oral communication, October 14, 1935.

² U. S. Geol. Surv., Mon. 32, pt. 2, 750, pl. 47, fig. 2, 1899.

³ *Loc. cit.*

⁴ *Loc. cit.*

⁵ Knowlton, U. S. Geol. Surv., Prof. Paper 130, 152, pl. 26, figs. 3-6, 1922.

Ceanothus sp.

(Plate 6, fig. 5)

One complete leaf constitutes the record of this species in the flora, and is distinctive enough in all its characters to be definitely referable to the living *Ceanothus cuneatus* Nutt. It is hardly believed justifiable to describe this species on the basis of one leaf impression.

Obovate in shape; apex retuse, narrowing to a cuneate base; 1.8 cm. long and 6 mm. wide; 5 mm. of a thick petiole present; midrib straight and stout; many secondaries departing at angles of 80°; tertiaries obscure; margin entire; texture coriaceous.

Although stated by Hollick to be not unlike *Ceanothus cuneatus*, *C. constrictus* Hollick¹ is much too remote in its resemblance to be considered similar to the Mount Eden species; it does, however, seem to foreshadow a *C. cuneatus* type. Several other Tertiary *Ceanothus* species have been described, but none show resemblance to this species.

Ceanothus cuneatus is the most wide-spread and characteristic species of the genus in southern California, especially in the lower and middle chaparral. It is distributed northward in the Coast Ranges and in the Sierra Nevada Mountains.

Collection—Univ. Calif. Mus. Pal., No. 1002.

ORDER SAPINDALES

Family ANACARDIACEÆ

Genus RHUS Linné

Rhus prelaurina n. sp.

(Plate 6, fig. 12)

Rhus sp. Dorf, Carnegie Inst. Wash. Pub. No. 412, 100-101, pl. 12, fig. 4, 1930.

Several fragmentary remains from the Orinda flora were referred to this genus by Dorf.² Of these, some of the impressions resembled *Rhus ovata* and others a *R. laurina* type. The basal three-fourths of a leaf in the Mount Eden flora is definitely referable to *R. laurina* and a description seems justified.

Description—Lanceolate-ovate in shape; base obtuse; apex absent; 5 cm. long, and 3.5 cm. wide; petiole absent; midrib straight and heavy; 13 alternate obtuse secondaries present, about half-way out recurving upward at 45°; tertiaries absent; margin poorly preserved, but entire; texture coriaceous.

Discussion—Of the fragments in the Orinda flora, that figured by Dorf³ seems to be of a *Rhus laurina* type. Only two other Tertiary *Rhus* species show any resemblance to this material. *Rhus mensæ* Cockerell (*R. metopoides* Lesquereux) from the Auriferous Gravels⁴ and the Florissant⁵ differs in a somewhat more ovate shape, but mostly in the secondaries, which enter the margin by conspicuous branchlets. A general similarity to *Rhus*

¹ Hollick, U. S. Geol. Surv., Mon. 50, 93, pl. 34, figs. 15-17, 1906.

² Carnegie Inst. Wash. Pub. No. 412, 100-101, pl. 12, fig. 4, 1930.

³ *Ibid.*

⁴ Lesquereux, Harvard Mus. Comp. Zool., Mem., vol. 6, 31-32, pl. 8, figs. 12, 13, 1878.

⁵ Cockerell, Amer. Jour. Sci., vol. 26, 543, 1908.

merrilli Chaney¹ is to be noted, but the secondary venation in that species is more open than in the Mount Eden form.

Rhus laurina is common throughout southern California in the lower chaparral and often mingles with sagebrush (*Artemisia* and *Salvia* spp.). It does not occur in the more arid interior region, except where it extends inland for a short distance along the larger river valleys. This *Rhus* requires an ameliorating coastal influence and reaches an optimum development in the coastal area. Near streams *Rhus* may be associated with species of oak, willow, poplar, sycamore, and walnut.

Collection—Univ. Calif. Mus. Pal., Holotype, No. 1003.

Family SAPINDACEÆ

Genus SAPINDUS Linné

Sapindus lamottei n. sp.

(Plate 6, fig. 6)

A complete, well-preserved, petrified seed and another smaller battered one constitute this record. In general detail of surface irregularities and ridging, in its micropyle, and in general shape, the complete seed shows a most remarkable resemblance to the modern *Sapindus drummondii* H. & A.

Description—Globose, slightly asymmetrical in shape; broadly rounded below and narrowing above; apex with a micropyle 1 mm. long, rendering the apex retuse; seed 1.0 cm. long and 9 mm. wide; several ridges commencing from the apex and apparent half-way down the seed; minor roughenings and corrugations all over the surface.

Discussion—Several Tertiary plant remains have been referred to *Sapindus drummondii*. Berry, in discussing the character of the Esmeralda flora,² considers *Sapindus* (*S. laciniifolius* Lesq.) indicative of a semiarid environment, and although not definitely stated, the reference was probably to *S. drummondii*. LaMotte,³ in a recent study of the genus *Sapindus*, believes that *S. spokaneensis* Berry of the Latah and Florissant is comparable to *S. drummondii*. He further suggests that *S. affinis* Newb.? of the Trout Creek, which was referred to *S. drummondii*, is more likely a variant of *S. oregoniana* Lesq., which resembles the living *S. mukorossi* Gaert. of eastern Asia. *S. oklahomensis* Berry in the florule of Brown County, Oklahoma, is also referable to *S. drummondii*.⁴

Sapindus is distributed through Arizona, New Mexico, and Sonora, and ranges eastward into southern Missouri. Westward, it is common along streams at lower elevations in semiarid areas, and often grows on open slopes and plains of broad river valleys. Among its associates in these regions are *Juglans*, *Ephedra*, *Platanus*, *Prosopis*, *Populus*, and *Salix*. This species is named in honor of Dr. R. S. LaMotte, who has recently completed a study of the fossil species of this genus.

Collection—Univ. Calif. Mus. Pal., Holotype, No. 1004.

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. 4, 125, pl. 16, figs. 1, 2, 1927.

² U. S. Nat. Mus., Proc., vol. 72, art. 23, 3, 1928.

³ Carnegie Inst. Wash. Pub. No. 455, 29-38, 1935.

⁴ Chaney and Elias, Carnegie Inst. Wash. Pub. No. 476, 1936.

ORDER GENTIANALES

Family OLEACEÆ

Genus FRAXINUS (Tourn.) Linné

Fraxinus edensis n. sp.

Description—Lanceolate in shape; tip acute, base acute-obtuse; larger leaflet 5.3 cm. long and 1.5 cm. wide, a smaller leaflet, with one side missing, measures 2.4 cm. long and 9 mm. wide (estimate); 5 mm. of petiole preserved, stout; midrib straight and stout below, becoming thinner and recurved in the apex, 5 alternate secondaries very long, the lower pair departing at 40° to 45° and rising abruptly to 80° and looping upward, camptodrome; secondaries with occasional marginal forking; intersecondaries present; tertiary venation irregular; entire- or finely serrate-margined; texture subcoriaceous.

Discussion—Most of the Tertiary *Fraxinus* species are definitely serrate-margined. The entire-margined *Fraxinus denticulata* Heer of the Bridge Creek¹ and *F. caudata* Dorf² from the Pliocene of California both differ from this species in their larger size, leaf base, and the number of secondaries, which also depart at different angles. The foregoing species are probably referable to the living *Fraxinus oregona* Nutt., while this species closely resembles *F. dipetala* H. & A.

Fraxinus dipetala is widely distributed through southern California and is a characteristic component of the chaparral on north slopes at middle altitudes. In such localities it is commonly associated with *Arctostaphylos*, *Ceanothus*, and *Cercocarpus*, and big-cone spruce is often in adjacent canyons. Along streams this ash may grow with oaks, willows, sycamores, cottonwoods, alders, and occasionally with walnuts. It ranges northward into the central Coast Ranges and the lower central Sierra Nevada Mountains.

Collection—Univ. Calif. Mus. Pal., Cotypes, Nos. 1005, 1006.

ORDER ASTERALES

Family COMPOSITÆ

Genus LEPIDOSPARTUM Gray

Lepidospartum sp.

(Plate 6, fig. 7)

One leaf is sufficiently distinct in all its characters to be provisionally assigned to this genus. The material was at first believed to represent *Baccharis*, but differences in venation would have rendered such a determination questionable. Although mature *Lepidospartum* shrubs often possess scale-leaves, occasional shrubs have been observed in full leaf along the edge of the Colorado and Mohave Deserts. The writer has also noticed that burning and cutting both result in profuse vegetating. No appreciable differences between the leaves of this species and the fossil material are apparent.

Obovate in shape; with a broadly obtuse apex, which narrows abruptly to a cuneate base; 2.2 cm. long and 1.6 cm. in width; petiole absent (mature leaves normally sessile); midrib slender, straight below and obscure and wavering near the apex; 5 subopposite secondaries departing at 60° to 70°

¹ Chaney, Carnegie Inst. Wash. Pub. No. 349, pt. 4, 132, pl. 19, figs. 5-7, 1927.

² Dorf, Carnegie Inst. Wash. Pub. No. 412, 106-107, pl. 13, figs. 6-8, 1930.

angles, very thin and straight, camptodrome near the margin; tertiaries very fine, reticulate; margin entire below, becoming serrate above; medium texture.

Lepidospartum squamatum is common in washes and on sand bars of the larger rivers throughout southern California, and is also abundant in the major watercourses of the deserts. This species, although best developed in southern California, extends northward in the Salinas River, the upper San Joaquin Valley, and the southern Sierra Nevada Mountains in Kern County.

Collection—Univ. Calif. Mus. Pal., No. 985.

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- FIG. 2—View of the City Creek Road at an elevation of 4700 feet, showing an association of *Pseudotsuga macrocarpa*, *Pinus coulteri*, and *Pinus tuberculata*. Associates in the immediate area include *Arctostaphylos glauca*, *Ceanothus cuneatus*, *Ceanothus divaricatus*, *Cercocarpus betuloides*, *Fraxinus dipetala*, and *Quercus chrysolepis*, while farther downstream *Lepidospartum squamatum*, *Salix exigua*, and *Salix lasiolepis* are present. All of these species are represented by equivalents in the Mount Eden flora.



FIG. 1



FIG. 2

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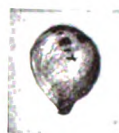
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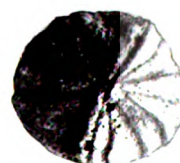
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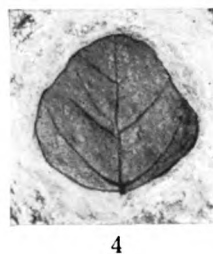
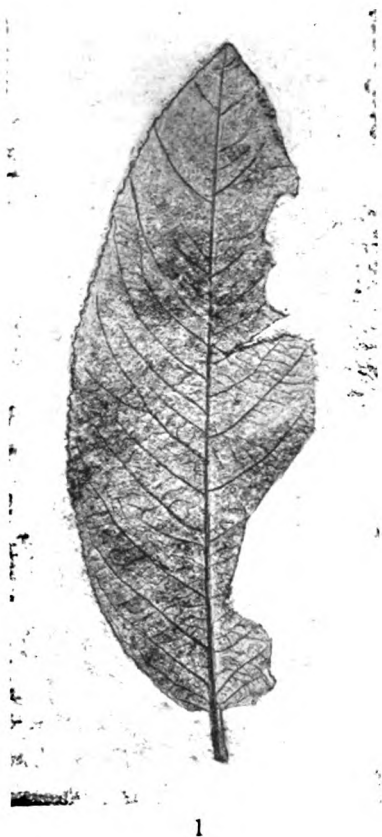
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CONTRIBUTIONS TO PALEONTOLOGY

IV

THE DESCHUTES FLORA OF EASTERN OREGON

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With seven plates

[Issued April 19, 1938]

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THE DESCHUTES FLORA OF EASTERN OREGON

INTRODUCTION

The Tertiary sequence in the John Day Basin and in adjacent areas of eastern Oregon supplies the most complete record of terrestrial deposits of this age in western America.¹ Mammalian faunas, although unknown from the Eocene, are well represented in beds of Oligocene, Miocene and Pliocene age. In the Eocene Clarno formation, in the Upper Oligocene or Lower Miocene John Day Series, and in the Upper Miocene Mascall formation, fossil plants are numerous and widely distributed. The paucity of the record of Pliocene vegetation is not surprising since most pyroclastic deposits of later Tertiary age have a texture too coarse to favor the preservation of leaf impressions. Another significant factor in restricting the record of Pliocene vegetation has been the relatively arid climate during this epoch. Both the lithology of Pliocene formations, and the character of their mammalian faunas, appear to indicate reduced precipitation as compared with Miocene and earlier deposits. Nowhere in western America are Pliocene plants as numerous as those of the Miocene. The reduced number of trees in semi-arid habitats and the increasing obstacles to preservation imposed in a region where the water table is lowered, are among the factors involved in their scarcity. The general picture outlined for the Pliocene epoch in the Columbia Plateau Province has involved gradual uplift of the Cascade Range, reduction of precipitation on its eastward flanks, and a resulting habitat too dry to permit continued occupation of this region by the forests which characterized eastern Oregon and Washington up to the end of the Miocene period. The absence of fossil plants from the Pliocene Rattlesnake formation of the John Day Basin and adjacent Oregon has therefore been consistent both with the local and with the more general physical setting on the western border of the continent during later Cenozoic time.

Within the past several years, construction of the Vanora Grade, on the Warm Springs cutoff of the highway from Madras to Portland, has opened a new and critical section of the Deschutes formation. This stratigraphic unit is widely distributed over the portion of the Columbia Plateau immediately east of the Cascades, as shown approximately on plate 1. Occurrence of fossil plants in the tuffs on the Vanora Grade was first reported by a highway engineer to Mr. Phil Brogan of Bend, Oregon. Subsequently, in cooperation with the State Highway Department, Dr. L. S. Cressman of the Uni-

¹ Merriam, Univ. Calif., Bull. Dept. Geol., vol. 2, No. 9, 1901; Merriam and Sinclair, Univ. Calif., Bull. Dept. Geol., vol. 5, No. 11, 1907; Merriam, Stock and Moody, Carnegie Inst. Wash. Pub. No. 347, III, pp. 43-92, 1925; Buwalda, Science, n. ser., vol. 66, No. 1701, pp. 135-136, 1927; Chaney, Carnegie Inst. Wash. Pub. No. 346, IV, pp. 47-138, 1927; Hodge, Pan-American Geologist, vol. 49, No. 5, pp. 341-356, 1928.

versity of Oregon visited the locality and made a critical collection of leaf impressions which I have had an opportunity to examine in his laboratory. In company with Mr. Brogan and Mr. Lewis H. Irving of Madras, I visited the locality during the summer of 1936, and secured the material on which this discussion is based. Acknowledgment is also due Carlton Condit of the University of California, and A. W. Hancock and A. D. Vance, members of the Geological Society of the Oregon Country, for their assistance in the field.

Following is the complete description of this occurrence:

Locality P3720—Vanora Grade, on the Warm Springs cutoff of the highway from Madras to Portland. At a point 9.7 miles north-northwest of Madras, in Jefferson County, leaf impressions occur at road level, and molds of tree trunks are exposed in the mudflow. Most of the specimens were collected from slabs thrown down the slope to the south, during highway construction in 1935.

THE GEOLOGIC OCCURRENCE OF THE FLORA

The Deschutes formation was first described by Russell who referred to it as the Deschutes sands.¹ Since there are volcanic rocks included in it, Williams later referred to it as the Deschutes formation.² Hodge subsequently found this name unsatisfactory, and substituted for it the name Madras.³ In his Madras formation are included also the Dalles beds and at least a part of the Satsop formation, which outcrop on opposite sides of the Cascades along the Columbia River at the north. There appears to be little question as to the accuracy of Hodge's reference of these three regional units to a single stratigraphic position, and it is possible that the name Madras formation may ultimately be acceptable for them collectively. In that case the unit here described may properly be termed the Deschutes member. For the present, it seems desirable to apply the previously used name to the rocks exposed in the area of the Deschutes drainage on the east side of the Cascades in central Oregon. The name *Deschutes formation* has the further advantage of being accepted by the Committee on Geologic Names of the United States Geological Survey.

In his discussion of the Geology and Water Resources of the Middle Deschutes River Basin, Oregon, Stearns has given the following description of the Deschutes formation:⁴

"Horizontal beds of yellow, brown and black partly consolidated sand, silt, gravel, and stratified fluvialite deposits of volcanic detritus, mostly basic, intercalated with and in most places capped by basalt flows. The

¹Russell, I. C., Preliminary report on the geology and water resources of central Oregon: U. S. Geol. Surv. Bull. 252, p. 90, 1905.

²Williams, I. A., Geology of the Pelton Dam Site, Oregon, unpublished report in the files of the Federal Power Commission.

³Pan-American Geologist, vol. 49, No. 5, pp. 350-352, 1928.

⁴U. S. Geol. Surv. Water-Supply Paper 637-D, p. 133, 1931.

lower basalt flow, more than 150 feet thick, is named the Pelton basalt member, and the upper flow, 25 to 150 feet thick, is for convenience referred to as the rim-rock basalt. Includes in a few places beds of white diatomite, which have a maximum thickness of 40 feet."

Both Stearns and Hodge mention the unconformable relations of this volcanic series upon older rocks, and emphasize its essentially horizontal structure.

The Deschutes formation is well exposed on Campbell Creek, a tributary of the Deschutes River, about 10 miles northwest of the town of Madras. Because of the relatively unconsolidated character of its pyroclastic and sedimentary members, the only conspicuous outcrops are those of lava flows except where road cuts have been excavated during the construction of the Vanora Grade. Pumiceous tuff and volcanic sediments outcrop at four cuts in a distance of 0.8 mile along the highway. The character of this material varies considerably over short distances. One of the most conspicuous members is a heavy, gray, pumiceous tuff¹ containing numerous bombs and angular fragments of lava up to 5 inches in diameter. It is near the base of this pumiceous tuff that most of the plant fossils occur. The detailed section is as follows:

50 feetBasic lava flows
75 feetTalus covered slope
10 feetCoarse volcanic conglomerate
6 feetCoarse, unassorted, pumiceous tuff with angular lava fragments. This layer varies in thickness laterally up to 15 feet.
16 inchesFine, unassorted, pumiceous tuff with abundant leaves on the basal bedding plane.
18 inchesCoarse to fine, pumiceous, cross-bedded, sandy tuff containing a few bent leaves.

In the course of road construction, many large blocks of the leaf-bearing tuff have been dislodged, and are lying on the slope below the highway. From these blocks, as yet unweathered, were secured most of the leaf fossils on which this report is based. They are especially numerous just above a layer of lapilli about an eighth of an inch thick; this separates the dense tuffaceous layer from the sandy, cross-bedded tuff below, near the base of the section described above. Unlike the leaves in the sandy material below, those resting upon the lapilli are flat lying. The lapilli average $\frac{1}{4}$ to $\frac{1}{2}$ inch in diameter, and are so closely spaced at some points on the bedding plane that they overlap. Other lapilli, mostly of smaller size, are scattered throughout the tuff.

¹According to Dr. C. A. Anderson, this is a pyroxene andesite crystal vitric tuff, containing crystals of feldspar, hypersthene and augite, and an undetermined microcrystalline aggregate. It is made up largely of coarse ash, with scattered pumice lapilli.

The presence of well preserved leaves in unassorted volcanic deposits of such coarse texture is sufficiently unusual to merit special consideration.¹ Their excellent state of preservation indicates that these leaves were not transported far after they were shed. Deposition in quiet water is suggested by their horizontal position on a bedding plane. In these respects they resemble fossil leaves of the Oregon Eocene and Miocene. In marked contrast, the matrices in which these older floras have been preserved are well assorted and relatively fine-textured.

Recent deposits laid down during and following the eruption of Mt. Katmai offer critical evidence as to the significance of these differences in lithology between the Deschutes and older volcanic sediments in eastern Oregon. The writer has not had an opportunity to visit the immediate vicinity of this Alaska volcano, and in the following comparisons has depended largely upon the writings and advice of Dr. C. N. Fenner. Following the Katmai eruption of 1912, there has accumulated in the vicinity of this volcano a thick series of coarse volcanic sediments, some of which show close resemblance to the Deschutes tuffs. These will be considered below. One hundred miles distant, on Kodiak Island, there were deposited ash layers which are more similar in texture to the Eocene and Miocene leaf-bearing deposits of eastern Oregon. Kodiak Island was first visited by the writer in 1913, some 16 months after the eruption. At that time most of the island was covered by ash. Subsequent detailed studies in 1936 have shown that most of the ash has been removed except on the lowlands. It has been concentrated there under conditions which throw light on the mode of deposition of the older plant horizons in the John Day Basin. Together with the data furnished by Fenner's extensive observations near the center of volcanic activity, the Kodiak studies suggest the manner in which leaves were most commonly buried during the Tertiary in western America, and provide an explanation for the abnormal mode of leaf accumulation in the Deschutes formation.

The eruption of Katmai in 1912 resulted in the covering of wide adjacent areas with volcanic ash. On the eastern end of Kodiak Island, 100 miles distant from the volcano, approximately a foot of volcanic ash was deposited during the eruption, in three distinct falls.² As recently observed there by the writer, after the passage of 24 years, this ash has been removed from most of the ridges and slopes on Kodiak Island.³ It remains as a layer 6 or 7 inches thick over much of the lower forested area at the east

¹ At only one other locality in western America are Cenozoic plant remains known to occur in such coarse tuffaceous deposits. This is the lower foothills of the Sierra Nevada about 3 miles southwest of Knights Ferry, in central California. The leaves are of different species from those in the Deschutes flora, but their preservation is identical, and the andesitic tuff in which they occur is closely similar to that on Vanora Grade. The age of these California deposits is considered to be Pliocene.

² Martin, G. C., *Nat. Geog. Mag.*, vol. 24, p. 166, 1913.

³ For a statement regarding the extensive removal of ash from Kodiak Island within 5 years after the Katmai eruption, see R. F. Griggs, *Ohio State Univ. Bull.*, vol. 24, No. 15, pp. 54-56, 1920.

end of the island, a layer now covered by an inch or more of moss and humus. Plant remains are generally absent from this sub-aerial deposit, although scattered spruce needles have been noted in it. From the mouths of such large streams as Buskin River, ash has been washed out and deposited along the shore for several miles. Along the lower courses of smaller streams, it has been accumulated in lake basins formed through the agency of beavers.

One of these, locally known as Silver Lake, lies near the eastern end of the island, 3 miles north of the town of Kodiak. It is 500 or 600 feet in diameter, with low surrounding slopes except at the northwest where a ridge reaches a height of some 50 feet. On the shallow shores, littered with angular fragments of slate, the ash deposit can be readily studied (see plate 4, fig. 2). In addition to several excavations dug through the ash to the gravel on the lake bottom, 3 cores were taken out at points 6, 8 and 10 feet from the shore. The deepest of these was 10½ inches long when dried, and several inches longer when collected. Thicker sections of the ash could have been secured farther out, but depth of the water made it impracticable, with the equipment available,¹ to collect core specimens more distant from the shore. In all of the samples of ash, plant remains in the form of leaves, cones, seeds and stems are common, and small beetles have also been found. A concentration of plant material was noted in the lower 5 or 6 inches of the ash section, with only scattered remains above. The material enclosing these more abundant remains is white and friable. It is fine-textured, the particles ranging in diameter from .08 to .1 mm. Associated bits of white pumice are .6 to .7 mm. in diameter. Thin layers of much finer and homogeneous white ash in one core include several alder and willow leaves. In general, the ash at the base of the section is angular and not well assorted. The ash in the upper part of the cores is medium coarse, ranging in size from .45 to .5 mm. It is gray in color, and differs further from that in the basal portion in the well assorted and rounded character of the grains. In considering the significance of these differences as related to the origin of the Kodiak ash, and as related to the problem of the origin of the Deschutes tuff, I am greatly indebted to Dr. Charles A. Anderson for advice based on his extensive studies of Tertiary and Recent volcanic deposits in western America.

Needles of Sitka spruce (*Picea sitchensis* Carr.) are most abundant in this quarter-century-old record of volcanic deposition. Defoliated twigs and seeds are common, and there are a few poorly preserved cones. The needles and seeds are preserved without apparent alteration, and in some cases have left well defined imprints in the enclosing ash. Such dicotyledonous leaves as alder (*Alnus sinuata* Rydb.) and willow (*Salix* sp.) are also represented in the ash, including both the highly fragile original material and faint impressions. Poorly preserved structures which may represent

¹ Sections of eave pipe of appropriate length were used for collecting these cores.

alder cones have been noted. Trees of all these species are now common on the borders of Silver Lake, and leaves recently shed are to be seen along the shore. These latter appear not to be entering the sedimentary record at the present time, except as a disorganized, carbonaceous litter which is accumulating at some points on the lake bottom. In fact, only scattered plant remains are present in the ash except near the base of the deposit. This lower portion of the ash section, comprising 5 or 6 inches of relatively fine and angular particles, is interpreted by the writer to represent material which fell upon the lake and settled to its bottom during the eruption. The enclosed leaves were concentrated here at the same time, when some of them may have been stripped from trees by falling ash and pumice. Wind and rain accompanying the eruption may have afforded unusual facilities for transportation of plant fragments to the lake basins. The overlying gray ash, which is somewhat more compact and coarse, is considered to have been washed into the basin subsequently, an origin which is consistent with the rounded shape of the ash particles. During this relatively slow accumulation, most of the leaves which were deposited on the lake bottom were decomposed, as is the case with leaves now falling into the lake. The mode of accumulation above outlined is considered to have involved the deposition of such abundantly plant-bearing beds as the John Day formation of Oregon, and the Florissant of Colorado. In the Bridge Creek shale member of the Lower John Day, fossil leaves are confined to definite zones a few inches to 2 or 3 feet in thickness; in these the ash particles are angular, with numerous evidences of direct fall during an eruption;¹ their texture is much finer than that of the Katmai ash. Above and below these leaf-bearing ash zones, the shale is coarser, shows evidence of weathering, and contains few or no leaf impressions. These barren deposits are considered to represent a secondary accumulation of ash brought in by streams and wind. Any leaves or other plant structures deposited in such sediments had a relatively slight chance of rapid burial and subsequent preservation. As in the case of leaves now blown into Silver Lake, disintegration appears to have preceded burial except in the case of such comparatively resistant objects as the needles of conifers. The abundance of needles—spruce in the recent deposits on Kodiak Island, redwood in the Bridge Creek shale—seems to be as much the result of resistant structure as of abundance in their contemporary forests.

Fenner reports the deposition of ash to a thickness of 10 or more feet at a distance of 8 to 10 miles from the crater of Katmai.² It is made up largely of pieces of light-gray pumice which range from minute size to dimensions of 3 or 4 inches. Its most obvious character is a well-defined stratification. In striking contrast are widespread unstratified deposits,

¹ Chaney, Carnegie Inst. Wash. Pub. No. 346, pp. 62, 91-93, 1927; Pub. No. 349, pp. 19-21, 1925.

² Jour. Geol., vol. 28, p. 596, fig. 17, 1920.

commonly overlain by beds of ash, which occur in adjacent valleys. Certain of these unassorted tuffs have been interpreted by Fenner as representing incandescent sandflows which issued from fissures in the valleys.¹ They have a thickness ranging from 10 to 200 feet, and averaging over 100 feet. Evidence of their high temperature at the time of emplacement is afforded by the carbonization of tree trunks with which they came in contact. In their lack of assortment and general physical aspect, the tuffs making up these sandflows closely resemble the leaf-bearing tuff of the Deschutes formation. Such a mode of origin for the latter seems, however, to be definitely precluded by the plant remains which occur in it. Such high temperatures as characterized the sandflows adjacent to Katmai would have reduced the stems to charcoal and would have resulted in the complete destruction of leaves. There is no evidence of carbon in the molds of the Deschutes tree trunks, and a test for carbon in the leaves was negative.² It is possible that the leaf-bearing portion of the Deschutes formation may have been derived from an incandescent sandflow which, after cooling, became saturated with water and moved on down the valley to a site of permanent deposition. But no direct emplacement of such a sandflow can be considered to have given rise to the Deschutes tuff in view of evidence of its low temperature conditions during accumulation.

Fenner has described another type of unstratified tuff which occurs as a relatively thin valley fill at many points adjacent to Mt. Katmai.³ This he considers to represent material which slid or flowed down from the valley slopes where it had previously accumulated; its motion appears to have been induced by volcanic earthquakes. The material composing these boulder flows, or boulder slides, in the Katmai region appears to have been largely derived from weathered rock which covered the slopes, since the boulders and smaller fragments are in many cases well rounded. Large amounts of pyroclastic material are also included. The field relations of the Katmai ash to these boulder flows indicate that most of them were closely associated with the eruption. Figure 2 on plate 2 shows a boulder flow which came down Mageik Creek from the slopes of Mt. Katmai and spread over the floor of Katmai Valley. The low temperature of this material is indicated by the unburned condition of the trees whose trunks have been buried to a depth of probably less than 10 feet. It is of interest to note that these trees are poplars, the most common genus in the Deschutes tuff.

While there are certain differences between these boulder flows of the Katmai area and the leaf-bearing tuffs of the Deschutes formation, they have in common a lack of assortment, a dominance of volcanic rocks, and

¹ *Ibid.*, pp. 576-583; Papers from Geophysical Laboratory, Carnegie Inst. Wash., No. 480, 1923.

² Acknowledgment is made to C. G. Maier, Director of the Pacific Experiment Station of the U. S. Bureau of Mines, who made this test.

³ *Jour. Geol.*, vol. 33, pp. 126-128, 1925.

evidence of low temperature at the time of deposition. The leaf-bearing layer of the Deschutes tuff is made up of relatively fine material, containing no well rounded fragments, and composed almost entirely of fresh pyroclastic rocks. However, an overlying 10 feet of volcanic conglomerate consists of rounded boulders, and may well have accumulated under conditions identical with those on the slopes and floor of Katmai Valley. The leaf-bearing tuff is considered to represent pyroclastic material originally deposited in well assorted layers on the valley slopes; becoming saturated, this material slumped down into the valley where it spread out, with fragments of all sizes intermixed, and buried the surface to a depth of 6 to 15 feet.

In the cut on Vanora Grade, the close association of pumiceous tuff, cross-bedded sands and grits, diatomaceous ash, volcanic conglomerate, and lava flows is indicative of highly varied conditions of accumulation over a relatively restricted area. This is consistent with the general picture here being developed, of a volcano whose flanks were littered with volcanic ejecta which slumped and were washed into valleys below. Except for a few twisted leaves in the cross-bedded sandy tuff immediately below the leaf zone, plant remains are entirely confined to the pumiceous tuff layer. Most of the leaves occur at its base, just above a layer of pumiceous lapilli. This leads to the suggestion that immediately following a major eruption, which scattered coarse lapilli over an adjacent valley, there was an extensive fall of leaves. The relatively complete preservation of the blades and petioles of these leaves indicates that few of them were cut off from the boughs by falling fragments of tuff. Rather it seems preferable to assume either that normal autumnal leaf fall, or perhaps a premature fall due to the destruction of trees by volcanic agencies, was responsible for their accumulation above the layer of lapilli. The concentration and horizontal position of most of the leaves at the base of the tuff suggest that they fell into a body of water, probably a small lake. Their excellent state of preservation indicates that almost immediately thereafter, this water body was filled by a mudflow from the slopes above. A few twisted leaf impressions above the major leaf zone represent leaves picked up and carried for short distances by this mudflow. But most of them were buried without distortion, and have been preserved between the base of the mudflow and the layer of pumiceous lapilli. Several tree trunks have been preserved *in situ*, as molds in the mudflow. The preservation of these to a maximum height of 15 feet is suggestive of rapid accumulation of the material which slumped down into the valley where they lived. Absence of plant remains from the associated fluvatile deposits appears to have been due to less favorable conditions for burial than were afforded by the rapid accumulation of the mudflow. The associated diatomaceous ash is too poorly compacted to afford suitable conditions for leaf preservation.

There are doubtless other methods by which unassorted tuff like that containing leaves in the Deschutes formation may be accumulated. However, on the basis of our present interpretation of this occurrence, the following general conclusions may be reached regarding its origin:

(1) The coarse texture of the larger constituents indicates a site of deposition within a short distance, probably not more than 2 or 3 miles at most, from a center of active vulcanism.

(2) Close association of most of the leaf impressions above a layer of pumiceous lapilli suggests a short time interval between an initial phase of the eruption and deposition of the leaves.

(3) The position of the leaves parallel to the bedding plane, and their excellent state of preservation, indicate accumulation in quiet water not far from the point where the trees from which they fell originally grew.

(4) The unassorted character of the overlying tuff is not consistent with an origin involving direct volcanic fall, or transportation to the site of deposition by running water or wind. It appears rather to represent an accumulation brought down as a mudflow from upper slopes adjacent to the volcano. The nature of preservation of leaves and trunks shows that this mudflow did not have a high temperature.

(5) The difference between the Deschutes mode of leaf occurrence and that of older fossil floras in adjacent Oregon appears to be bound up in its closer proximity to the source of volcanic material. The leaves of the Clarno, John Day and Mascall formations occur in fine, well assorted ash which was probably carried a considerable distance through the air before it fell, as in the case of the modern deposits on Kodiak Island. The leaves of the Deschutes formation were buried in a coarse, unassorted tuff which could have accumulated only a short distance from the volcano, as in the case of the modern deposits on Mageik Creek. Such a situation is in complete agreement with the environmental conditions suggested by the trees represented in the Deschutes flora, which will be described below.

COMPOSITION OF THE FLORA

The Deschutes flora as now known is made up of the following species:

Populus pliotremuloides Axelrod
Populus alexanderi Dorf
Salix florissanti Knowlton and Cockerell
Prunus irvingi new species
Acer negundoides MacGinitie

This small number of species is consistent with the general climatic picture which has been suggested, and which will be further considered below. In semi-arid regions of western America today, woody plants are largely confined to stream borders. This rather uniform habitat tends to reduce the total number of tree and shrub species, at least in situations where leaves

and other plant structures may readily enter the fossil record. In such higher situations as the Blue Mountains, the variety of woody plants is greatly increased; but the remains of these mountain trees and shrubs rarely enter the sedimentary record since they are too remote from sites of deposition.

With the exception of a single samara of box elder, all of the determinable fossils collected are leaf impressions. In addition there are casts of trunks of small trees which may represent more than one fossil species, but most nearly resemble, in size and proportions, the stems of the modern aspen, *Populus tremuloides* Michaux. Such a reference is substantiated by the predominance of leaves of *P. pliotremuloides* in the Deschutes tuff.

Populus pliotremuloides has been described by Axelrod from the Mt. Eden beds of southern California, which are assigned to the Middle Pliocene on the basis of plant fossils and associated mammals.¹ This fossil aspen is represented by leaves which closely resemble those of the modern *P. tremuloides*. They are of smaller average size than those of the living species, but are almost identical in size with those of trees growing in drier situations. Larger and thinner leaves of a poplar of the *tremuloides* type have been described as *P. lindgreni* Knowlton from several Upper Miocene localities in Oregon, Idaho and Nevada.² Another related fossil species, *P. delicatus* Chaney, from the Lower Miocene Eagle Creek flora of northern Oregon,³ has small, thin leaves. *P. eotremuloides* Knowlton, from the Payette of Idaho, was considered by Knowlton to represent an ancestral type of *P. tremuloides*.⁴ More recently it has been recorded from the Upper Cedarville flora of Nevada, and has been considered to be more nearly related to the living *P. trichocarpa* Torrey and Gray.⁵ The larger size and thinner texture of leaves of the Miocene aspen, *P. lindgreni*, are consistent with the relatively humid climate which characterized this epoch in western America. All of them are readily distinguishable from *P. pliotremuloides*.

Populus alexanderi was described from beds of Pliocene age at various localities in California by Dorf,⁶ who pointed out its resemblance to the living *P. trichocarpa*. A survey of Dorf's types indicates that he may have included under this species several specimens which, from their greater resemblance to the living *P. fremontii* Watson, should have been referred to his *P. prefremontii*. In any case there are specimens from several California localities, notably in the northern part of the state near Alturas, which closely resemble *P. trichocarpa*. In our collections from the Deschutes tuff, leaves of *P. alexanderi* are relatively scarce. They tend to be

¹ Carnegie Inst. Wash. Pub. No. 476, III, p. 169, 1937.

² Knowlton, U. S. Geol. Surv., 18th Ann. Rept., pt. 3, p. 725, 1898; U. S. Geol. Surv. Bull. 204, p. 29, 1902. MacGinitie, Carnegie Inst. Wash. Pub. No. 416, p. 49, 1933.

LaMotte, Carnegie Inst. Wash. Pub. No. 455, V, p. 115, 1936.

³ Contr. Walker Museum, vol. 2, No. 5, p. 162, 1920.

⁴ U. S. Geol. Surv., 18th Ann. Rept., pt. 3, p. 725, 1898.

⁵ La Motte, Carnegie Inst. Wash. Pub. No. 455, V, p. 114.

⁶ Carnegie Inst. Wash. Pub. No. 412, I, p. 75, 1933.

smaller in size and thicker in texture than leaves of this species from the California Pliocene. They are definitely smaller and thicker than the leaves of *P. eotremuloides* from the Miocene of Idaho and Oregon, which occur in a flora indicating a more humid climate than that of the Deschutes stage.

Fossil willows, like modern species of the genus, are difficult to distinguish on the basis of their leaves alone. In referring the Deschutes willow leaves to a previously described species, *Salix florissanti* Knowlton and Cockerell, an effort is made to avoid undue multiplication of species in a genus already over-expanded. *S. florissanti* has been reported from a wide range of Miocene localities, including Florissant, Colorado, the Mascall and Latah formations of Oregon and Washington, and corresponding deposits in Idaho. It is also present in the flora of the Dalles formation, which appears to be related in age to the Deschutes formation. The stratigraphic significance of the occurrence of this Miocene species in the Deschutes formation is probably slight, for it appears to have survived with little change from the Miocene to the present, in the area east of the Cascade Range. A similar living species, *S. caudata* (Nutt.) Heller, is common as a shrub or small tree along stream borders in eastern Oregon.

Like most of the vegetation from the Deschutes formation, the leaves of *Prunus irvingi* indicate a less favorable environment than was prevalent during Miocene and earlier time. They are smaller than any leaves of this genus previously described from western America, and are relatively coarse in texture. In general appearance they most closely resemble the smaller leaves of *P. coveus* Chaney from the Lower Miocene of the Crooked River Basin.¹ Both these fossil species appear to be related to the living *P. emarginata* Walpers, which grows as a shrub in the drier parts of western America, or as a small tree on the more humid coastward slopes. The size and texture of the leaves of this living species vary greatly according to the habitat, including larger leaves of the *coveus* type and small ones like *irvingi*. Clearly a question may be raised as to the propriety of assigning separate names to these two types of fossil leaves which are included within the range of variation of one similar modern species. Since they appear to represent two distinct habitats which were widespread in eastern Oregon at successive epochs of the Tertiary, there is at least an ecologic and a stratigraphic basis for considering *P. irvingi* as a species distinct from *P. coveus*. Although in size and texture it approaches *P. masoni* La Motte from the Upper Miocene deposits of northwestern Nevada,² *P. irvingi* shows marked differences in venation. None of the other fossil species of cherry from western America are sufficiently similar to warrant comparison with the Deschutes species.

¹ Carnegie Inst. Wash. Pub. No. 346, IV, p. 123, 1927.

² Carnegie Inst. Wash. Pub. No. 455, V, p. 131, 1936.

Acer negundoides is represented in the Deschutes flora by several leaflets and a samara. There is little basis for distinguishing these fossil remains from corresponding structures of the living *Acer negundo* Linnæus and its varieties. Although widely distributed in the West at the present time, box elder trees are seldom numerous. A similarly widespread but scattering distribution appears to have characterized its Tertiary equivalent in western America. It has been recorded from the Upper Oligocene or Lower Miocene Bridge Creek flora of the John Day and Crooked River Basins of eastern Oregon,¹ from the Lower to Middle Miocene Eagle Creek formation of the Columbia River Gorge,² from the Upper Miocene Trout Creek flora of southeastern Oregon,³ from beds of similar age at 49 Camp, Nevada,⁴ from the Idaho formation of western Idaho which is considered to be transitional between the Miocene and Pliocene,⁵ and from the Ogallala formation in western Oklahoma in beds transitional between the Lower and Middle Pliocene. Except for single leaflets at the Nevada and Oklahoma localities, the record of *A. negundoides* to date has been entirely of its winged seeds. In the Dalles formation of north central Oregon, leaflets and seeds are abundantly represented. The flora of this formation, shortly to be described, is considered by the writer to indicate a Pliocene age.

Table 1 summarizes the relationships of the fossil species to those now living, and gives the present day distribution of these modern equivalents.

TABLE 1

Fossil species	Related living species	Occurrence
<i>Acer negundoides</i>	<i>A. negundo</i> * <i>A. negundo</i> †	Rocky Mountains Central to Southern California
<i>Populus alexanderi</i>	<i>P. trichocarpa</i>	Alaska to California, east to northern Rocky Mountains
<i>Populus pliotremuloides</i>	<i>P. tremuloides</i>	Most of North America
<i>Prunus irvingi</i>	<i>P. emarginata</i>	British Columbia to California, east to Rocky Mountains
<i>Salix florissanti</i>	<i>S. caudata</i>	British Columbia to California, east to Rocky Mountains

* var. interior.

† var. californicum.

All of these related modern species, with the exception of the box elder, may be found living together in mountain valleys of eastern Oregon, within a

¹ Brown, Jour. Paleont., vol. 9, No. 7, p. 580, 1935.

² Brown, U. S. Geol. Surv., Professional Paper 186, p. 180, 1937.

³ MacGinitie, Carnegie Inst. Wash. Pub. No. 416, II, p. 62, 1933.

⁴ LaMotte, Carnegie Inst. Wash. Pub. No. 455, V, p. 136, 1936.

⁵ Dorf, Carnegie Inst. Wash. Pub. No. 476, II, p. 121, 1936.

few miles of the fossil locality. The absence of *A. negundo* is difficult to explain, but raises no inconsistencies of distribution or association, since this tree occurs regularly with the modern equivalents of Deschutes species in other parts of western America. Of interest in this connection is the record of its presence in northwestern Nebraska; Clements has noted box elders growing within half a mile of relict aspens in the sand hills.¹ I have recently seen box elders near Verdi, Nevada, in a situation which suggests that they are indigenous. All of the other Deschutes genera occur nearby, although *Populus tremuloides* has not been observed at so low an elevation.

The relationships of the fossil species to the living species of their genera in western America are sufficiently close to provide critical information regarding the physical setting in eastern Oregon during the Pliocene epoch.

PHYSICAL CONDITIONS INDICATED BY THE FLORA

In a preceding chapter, the conditions of deposition of the volcanic sediments of the Deschutes formation have been discussed, and comparisons made with the mode of origin of similar sediments which have accumulated recently near Mt. Katmai, Alaska. The geographic distribution of modern equivalents of the species in the Deschutes flora has also been considered. To reconstruct the environment in eastern Oregon during the Deschutes stage, this evidence regarding the origin of the sediments may be combined with the physical indications of the flora.

The most critical characters of the tuff in which the leaves occur are its coarse texture and its lack of assortment. Both of these suggest a site of deposition not far distant from the volcano which was the source of the ash and pumice in which the plant remains were buried. If the habitat of the Deschutes flora was one of relatively high altitude and relief, as compared with those in which other Tertiary floras in eastern Oregon have been accumulated, the plants themselves should offer corroborative testimony. No floristic evidence for an upland habitat could be more convincing than that of *Populus pliotremuloides*. Outnumbering by a wide margin all of the other species in the flora, this Pliocene aspen may be considered to indicate an environment essentially like that of its modern equivalent, *P. tremuloides*, which is limited to mountain slopes in Oregon at the present time. According to Jepson,² the aspen has a more extensive distribution than any other tree on the continent, especially in high latitudes, where it reaches nearly to sea level. Extending along the Cordillera into Mexico, it is confined southward to progressively higher altitudes. Two varieties of the American aspen have been designated by Sargent,³ but such authorities as Abrams,⁴ Jepson and Sudworth⁵ do not recognize them. Sudworth makes the following statement regarding the occurrence of the aspen in Oregon:

¹ Oral communication, April 1937.

² Manual of Flowering Plants, p. 269, 1925.

³ Manual of Trees of North America, pp. 121-122, 1922.

⁴ Illustrated Flora of Pacific States, p. 486, 1923.

⁵ Forest Trees of Pacific Slope, pp. 239-244, 1908.

"In Blue Mountains, occasional groups in open spaces on high ridges. Forms part of undergrowth in yellowpine forest on east slope of Cascades—nowhere abundant. In south Oregon, as a small part of stand, and much scattered; in thickets about springs, occasionally over large areas of semi-arid land."

My own observations in the Ochoco and Blue Mountains adjacent to the John Day Basin add further information regarding the habitat and associates of the aspen. In this region it occurs along streams in open valleys, on the plateau and mountain borders, at elevations from 3000 to 3700 feet above sea level. Here it is associated with alder (*Alnus tenuifolia* Nuttall), birch (*Betula fontinalis* Sargent), black cottonwood (*Populus trichocarpa*), cherry (*Prunus emarginata* and *P. demissa* Walpers), dogwood (*Cornus glabrata* Benth), elderberry (*Sambucus racemosa* Linnaeus), service berry (*Amelanchier alnifolia* Nuttall), syringa (*Philadelphus lewisii* Pursh), and willows (*Salix caudata* and *S. monochroma* Ball). Juniper (*Juniperus occidentalis* Hooker) and sage (*Artemisia tridentata* Nuttall) occupy the upper slopes, and may extend down almost to the valley flats, as shown in figure 2 on plate 5. Aspens are also well represented in the yellow pine (*Pinus ponderosa* Lawson) forest, at an elevation of 4000 to 5000 feet above sea level. Even here, in a relatively moist habitat, they are most numerous along streams and on the slopes adjoining. In addition to yellow pine, the associates of the aspen at these higher levels are alder, birch, black haw (*Crataegus douglasii* Lindley), cherry, Douglas fir (*Pseudotsuga taxifolia* Britt), grand fir (*Abies grandis* Lindley), larch (*Larix occidentalis* Nuttall), and willows. This higher habitat is pictured in figure 1 on plate 5.

From the composition of the fossil flora, it may readily be determined that the lower of these modern habitats corresponds more closely to the Deschutes site of deposition than the upper. Although the Pliocene equivalent of the aspen is the dominant element of the flora, there is a sufficient representation of *Populus alexanderi* to indicate that this additional species of poplar lived at no great distance. Its modern equivalent, *P. trichocarpa*, attains its greatest size and abundance in eastern Oregon along the floodplains of the John Day River and other large streams, at an altitude of about 2000 feet. Since it is not numerous above 3300 feet, the normal habitat of the black cottonwood is readily distinguishable from that of the aspen. However, the overlapping of the ranges of these two species of poplar between 3000 and 3500 feet, and rarely up to 3750 feet, provides a zone in which both occur, with the aspen always more abundant. This appears to be essentially the situation under which the leaf-bearing tufts of the Deschutes formation were accumulating, with leaves of *P. plotremuloides* outnumbering those of *P. alexanderi* by a ratio of a hundred to one.

The black cottonwood has not been recorded at the higher levels where the aspen occurs in association with conifers as above listed. The absence

of these conifers from the fossil record is additional evidence that the Deschutes habitat corresponded more closely to the lower than to the upper levels of aspen distribution. Fossil remains of *Abies*, *Pinus* and *Pseudotsuga* are regularly found in Miocene floras of Oregon. Pine needles and scales are abundantly represented in the contemporary deposits of the streams in the mountains of eastern Oregon, and their presence in the Deschutes tuff would appear to have been inevitable if the Pliocene equivalent of the yellow pine had lived near the site of deposition.

Since modern equivalents of the fossil cherry and willow live today throughout the range of the aspen and under even more varied conditions, the occurrence of *Prunus irvingi* and *Salix florissanti* in the Deschutes flora has no bearing on the question of altitude. The modern equivalents of *Acer negundo* var. *interior*, and *A. negundo* var. *californicum*, are also rather widely distributed in altitude. The evidence of the poplars, without reference to these other less definitely zoned species, is sufficiently exact to indicate that the climate at the Deschutes site of deposition was essentially like that of today in eastern Oregon at or about 3000 to 3500 feet. The nearest locality to Vanora Grade where aspens have been observed is about 30 miles to the southeast, in the Ochoco Mountains at an elevation of 3700 feet. The recorded annual precipitation at Ochoco, an adjacent station of the United States Weather Bureau, is 17.16 inches; the rainfall is doubtless lower at the point where aspens were noted, for Ochoco has a higher elevation. No rainfall data are available for another situation where aspens have been noted, on the plateau above Mitchell, some 50 miles east of the fossil locality. This situation, at an elevation of 3400 feet, appears to approximate closely the Deschutes habitat, with an association of dominant aspen, together with black cottonwood, cherry and willow. On the plateau above Fossil, 40 miles northeast of Vanora Grade, one large cottonwood is associated with numerous aspens, as well as cherries and willows. Here at an elevation of 3100 feet, the annual rainfall is estimated as not less than 14 inches.¹ The precipitation as recorded at Madras, a short distance from the fossil locality, is only 8.53 inches a year. It seems reasonable to conclude that during the Deschutes stage, when aspens were abundant at this level, the rainfall was at least 5 inches higher than at present.

This reduction in rainfall at Vanora Grade since the Pliocene may be explained in two ways. Down-warping of the region might be expected to bring lower precipitation and to have resulted in the elimination of aspens from the modern vegetation. However, it appears unlikely that a lowering of 1000 to 1500 feet could have been accomplished without more definite evidence of folding in the Deschutes formation. A more probable cause for

¹ At the nearby town of Fossil, some 400 feet below, the average precipitation is 13.23 a year.

the climatic change may lie in topographic adjustments to the west during later Cenozoic time.

As above indicated, a general trend toward aridity has been observed at many points in the Columbia Plateau and Great Basin Provinces as a result of the progressive uplift of the Cascades and the Sierra Nevada. Elimination of the stream border vegetation from the vicinity of Vanora Grade, and its survival at levels 1000 to 1500 feet higher, in the Ochoco and Blue Mountains, is consistent with this trend. Similar shifts in distribution during the Tertiary period, involving changes in both altitude and latitude, have characterized most of the Cenozoic floras which have been studied in western North America.

As elsewhere described, the relatively small size of the *Deschutes* leaves and their thick texture are consistent with a habitat in which optimum conditions of water supply are not present. Especially in the case of the fossil poplars and cherry, a reduction in leaf size and an increased thickness may be noted when they are compared with corresponding species from the Miocene of eastern Oregon. In these characters the fossil leaves resemble those of related living species in situations where the minimum amount of moisture is available.

The factor of altitude is of critical importance in any consideration of fossil vegetation, not only because it affects climate, but also because it largely determines whether plant structures may be preserved in the sedimentary record. One of the reasons why Pliocene floras are seldom found in semi-arid regions of the western United States is that woody plants appear rarely to have been living near Pliocene sites of deposition. At higher levels, where there was sufficient rainfall to support abundant woody plants, there was no accumulation of sediments in which their leaves, fruits and stems might be buried. At lower levels, where streams were actively depositing, trees were relatively few in number; and here the long season of drought resulted in drying out of the sediments in which leaves may have been buried, resulting in their partial or complete destruction. In a region with such climate, the particular combination of circumstances which favors preservation of leaves—sufficient precipitation to permit the growth of trees and shrubs on the borders of a permanent stream, and rapid deposition of sediments to bury plant structures—may best be met in the vicinity of a volcano from which large amounts of pyroclastic material are expelled. Even here, the tuff is commonly too coarse, and lava flows may be too closely associated, to permit a permanent record of leaf impressions in the sediments. At such higher altitudes erosion may be so rapid as to remove unconsolidated or only partly consolidated pyroclastic deposits. As a result of exceptionally favorable conditions for plant growth and leaf burial at the Vanora Grade locality during the Pliocene, leaves were enclosed in great numbers at one level, in spite of the relative coarseness of the *Deschutes* tuff. The volcanic peak from which it was ejected has since been destroyed

by erosion, but the partly consolidated tuff, protected by an overlying flow of basalt, has not yet been removed from the Vanora Grade locality, or from a wide area on the plateau fronting the east slope of the Cascades. Only a nice adjustment of topography, climate and comparatively late geologic age has made possible the accumulation of these fossil plants, and the survival of the beds containing them in this area.

The rarity or absence of leaf impressions from the Pliocene record in other parts of eastern Oregon indicates that the above described conditions were highly localized. The widely exposed and extensively studied Rattlesnake formation of the John Day Basin is not known to contain fossil plants, although it includes layers of rhyolitic tuff which appear to have presented a more suitable medium for burial than the andesitic tuff of the Deschutes formation. Evidence that the Rattlesnake formation may have been accumulated at a lower altitude, where precipitation was insufficient for the growth of aspens, is afforded by the mammalian fauna described by Merriam, Stock and Moody.¹ This includes such horses as *Pliohippus* and *Hipparion*, and remains of antelope and proboscideans, all of which suggest a plains rather than a mountain habitat. Relations of certain of its faunal elements with Pliocene faunas of the Pacific Coast Province have been pointed out,² and further suggest a lowland rather than an upland as the site of accumulation of the Rattlesnake formation. However, there is no structural evidence for assuming that this formation has been greatly uplifted since its deposition; and since its present altitude is about 2200 feet, essentially that of the Vanora Grade plant locality, its position above sea level at the time of deposition may not have been greatly different from that of the Deschutes. Local differences in topography may have prevented the occurrence of aspens near the sites of Rattlesnake deposition; and a greater distance from sources of the pyroclastic material may have precluded their preservation in the record. It is even possible that plant remains may ultimately be found in some particularly favorable situation in the Rattlesnake formation, in which case they may be expected to show a close relationship to the Deschutes flora.

Summarizing the evidence suggesting the physical setting in the vicinity of Vanora Grade during the deposition of the Deschutes formation, the following considerations may be mentioned:

(1) The coarse texture of the tuff and the abundance of pumiceous lapilli suggest close proximity to a volcano. Associated volcanic conglomerates and sands indicate a region of high relief, while local deposits of diatomite suggest adjacent lake basins.

(2) The composition of the flora, especially the dominant *Populus plicatula*, is indicative of a cool, semi-arid climate in which trees were largely restricted to stream borders at relatively high elevations.

¹ Carnegie Inst. Wash. Pub. No. 347, III, 1925.

² *Ibid.*, p. 60.

(3) In view of the absence of the Deschutes genera from Vanora Grade, at the present time, and of the restriction of modern aspens to levels 1000 to 1500 feet higher, it may be concluded that there has been a change in climate involving a reduction in annual rainfall of 5 inches or more since the Deschutes stage.

(4) The general setting in which the Deschutes flora lived may best be reconstructed by a survey of the stream border vegetation in and adjacent to the Ochoco and Blue Mountains a few tens of miles distant from the fossil locality. With the exception of box elder, all of the fossil species have common modern equivalents in the bottoms of broad open valleys such as that shown in figure 2 on plate 5. The conditions under which the Deschutes formation was accumulated appear to have been duplicated during the eruption of Mt. Katmai in 1912. In its immediate vicinity there were accumulated tuffaceous sediments which resemble in texture and other physical characters the leaf-bearing tuffs of the Deschutes formation.

THE AGE OF THE DESCHUTES FLORA

In the case of a flora comprising only 5 forms, the common method for determining the age of a formation through a study of the stratigraphic range of its fossil species is not wholly adequate. This method is even less appropriate in the case of a flora such as the Deschutes, in which all the species have survived with little apparent modification to the present day. It is clear that an analysis of the age of the Deschutes flora along other than strictly stratigraphic lines may furnish critical supplementary evidence regarding its age. Before considering this evidence, however, it is desirable to summarize briefly the recorded occurrence of the Deschutes species, and of species related to them.

TABLE 2—*Stratigraphic Distribution of the Deschutes Flora*

Fossil species	Miocene					Transi- tional	Pliocene			
	Florissant, Colo.	Latah, Wash.	Mascall, Ore.	Trout Creek, Ore.	Upper Cedarville, Nev.	Idaho Beds, Ida.	Ogallala, Okla.	Mt. Eden, Calif.	Sonoma, Calif.	Alturas, Calif.
<i>Acer negundoides</i>	X	X	X	X	X	X
<i>Populus alexanderi</i>	X	X	X
<i>Populus pliotremuloides</i>	X	X
<i>Salix florissanti</i>	X	X	X

A survey of the distribution of the 4 species previously known indicates that 2 of them occur in the Miocene and 3 in the Pliocene beds of western America.

Of the Miocene species, *Acer negundoides* occurs also in the Pliocene of Oklahoma, and in transitional beds in Idaho; it is abundant in the Dalles beds in north central Oregon, which are considered by the writer to be of essentially the same age as the Deschutes formation; it has survived in essentially unmodified form in the Rocky Mountains and in California. The second Miocene species, *Salix florissanti*, has not been previously recorded from beds of younger age. It differs from the leaves of the common Pliocene willow, *S. coalingsensis*, in having a definitely serrate margin, and in having more numerous secondaries which leave the midrib at lower angles. However, these distinctions are none too constant,¹ and some question may remain as to the propriety of separating the two fossil species on the basis of their leaves alone. The fact that a modern species of willow, *S. caudata*, now living in eastern Oregon, has leaves indistinguishable from those of *S. florissanti* further emphasizes the lack of any great stratigraphic significance in its occurrence in the Deschutes formation.

Of the 3 species with previously recorded Pliocene occurrence, *Acer negundoides* has, as above indicated, been found also in beds of Miocene age. The two species of poplar, *P. alexanderi* and *P. pliotremuloides*, are characteristic Pliocene species. Both of them appear to have been derived from larger and thinner-leaved Miocene species, of which *P. eotremuloides* shows ancestral relationship to *P. alexanderi*, and *P. lindgreni* to *P. pliotremuloides*. In view of the well established trend toward aridity in the Columbia Plateau Province during later Cenozoic time, the presence of these relatively xeric poplars in the Deschutes formation is an indication of its post-Miocene age. A similar relationship is apparent in the case of the fifth Deschutes species, *Prunus irvingi*, which is here described as new. Its leaves are smaller and more coriaceous than those of *P. coveus* from the Lower Miocene or Upper Oligocene Bridge Creek shales of the Crooked River and John Day Basins.

Any determination of the age of the Deschutes formation based upon floral evidence must take into consideration not only those Miocene species which have been recorded from it, but the genera and species regularly characteristic of the Miocene which are absent. Many Miocene floras have been studied in western America, all of which are composed of two or more of the following elements: (1) the mesic *Sequoia* (or *Taxodium*) element; (2) the broad-leaved deciduous element; (3) the Asiatic element; and (4) the border element. There is of course a considerable degree of overlapping between these elements. Although they represent broad-leaved deciduous genera, *Acer*, *Alnus*, *Cornus* and *Corylus* are considered under the *Sequoia* element because they regularly occur with the redwood in coastal Cali-

¹ Dorf, Carnegie Inst. Wash. Pub. No. 412, pl. 7, fig. 6.

fornia. For the purpose of emphasis, the broad-leaved deciduous element has been restricted to include only those genera which are now extinct in western America. Most of the genera of the broad-leaved deciduous element are present both in the living forests of the eastern United States and of northeastern Asia. However, the Asiatic element as here defined includes only genera which no longer occur native in any part of North America, as well as certain species which are more similar to corresponding Miocene forms than are any living American species. It is significant that there is little or no overlap between the mesic *Sequoia* element and the border element.

These elements will be considered briefly in relation to the Deschutes flora:

(1) The redwood and its associates are so commonly present in western Miocene floras at middle latitudes as to represent their most characteristic element. In addition to *Sequoia* (of the *sempervirens* type), this element includes *Acer* (of the *macrophyllum* and *circinatum* types), *Alnus*, *Cornus*, *Corylus*, *Quercus* (of the *Lithocarpus densiflora* type) and *Umbellularia*. Such an assemblage reflects a climate in which extremes of temperature were lacking, and in which rainfall was abundant and generally distributed throughout the year. The absence of this element from the Deschutes flora suggests that these climatic conditions were no longer present in eastern Oregon when the Deschutes formation was deposited. This implies that the Cascade barrier to the east, which was formed for the most part during late Miocene and Pliocene time, had been folded up at least in part before the Deschutes stage.

(2) The broad-leaved deciduous element is made up of genera which no longer live west of the Rockies, but which have survived in the eastern United States. These include *Carpinus*, *Fagus*, *Liquidambar*, *Liriodendron*, *Ostrya*, *Tilia* and *Ulmus*, all of which now live in regions of summer rainfall, and shed their leaves at the beginning of the cold winter season. Their presence in eastern Oregon during the Miocene indicates that major climatic changes resulting from the uplift of the Cascades, and perhaps from other causes, had not yet been felt in this region. The absence of all these genera from the Deschutes flora indicates that new conditions had been introduced which made it impossible for them to survive.

(3) The Asiatic element: All of the broad-leaved deciduous genera mentioned above have survived as well in northeastern Asia, where a climate characterized by summer rainfall affords conditions essentially like those in the eastern United States. There are also living in northern China and Japan several genera such as *Cercidiphyllum*, *Ginkgo* and *Trapa* which do not occur in the modern vegetation of North America, but which were present in western America during the Miocene. In addition there are fossil species of such genera as *Acer*, *Castanea*, *Cratægus*, *Quercus*, *Tilia* and *Ulmus* which have their closest living specific equivalents in north-

eastern Asia. With the rise of the Cascade Range and the accompanying changes in climate, plants of this Asiatic element became rare in western America; few of them lived beyond the end of the Miocene and none are known to have survived the Middle Pliocene.

(4) The border element includes trees and shrubs whose modern equivalents now occupy slopes above the redwood forest proper, or live on its edges. In both these situations there is greater exposure, as reflected by the more xeric aspect of the vegetation growing there. In Lower Miocene floras of eastern Oregon, this element is subordinate in importance to the typical mesic *Sequoia* element, although in some situations it has been recognized as present.¹ By Upper Miocene time, a reduction in rainfall was already apparent,² and such border genera as *Acer* (of the *glabrum* and *negundo* types), *Arbutus*, *Populus* (of the *tremuloides* and *trichocarpa* types), *Prunus* (of the *emarginata* and *integrifolia* types), *Pseudotsuga*, *Quercus* (of the *chrysolepis* and *kelloggii* types), *Salix* and *Sapindus* are increasingly common.

It is evident that the border element is the only one of the Miocene units which is represented in the Deschutes flora. Its resemblance to Upper Miocene floras of the Columbia Plateau and northern Great Basin regions has already been emphasized. But the absence from it of the mesic *Sequoia*, the broad-leaved deciduous, and the Asiatic elements, and of most of the more southerly members even of the border element, such as *Arbutus*, *Sapindus* and the live oaks, suggests that it lived subsequent to Upper Miocene time, after the Cascade climatic barrier was well developed. Whereas the border element is only a part, and not always an important part, of the Upper Miocene vegetation, this element makes up the whole of the Deschutes flora.

In its size, composition and physical indications, the Deschutes flora more closely resembles those which have been recorded from the Pliocene of western America than any of older or younger age. Made up exclusively of trees and shrubs whose modern equivalents occupy stream borders in regions of only moderate precipitation, the Deschutes flora is strikingly similar in general aspect to the Ogallala flora from Beaver County, Oklahoma, and to several California floras which are also referred to the Pliocene age. The principal differences between it and the Ogallala flora involve the presence in that more southern floral unit of trees such as *Bumelia*, *Diospyros*, *Gymnocladus*, *Platanus* and *Sapindus*, and of a relict Asiatic element comprising *Ulmus* (*parvifolia* type) and possibly *Cercidiphyllum*. The Deschutes is unlike the more northern of the floras from the interior of California (Alturas, Orinda and Etchegoin) in that it contains no *Platanus* or live-oaks, again an expression of difference in latitude. The Mt. Eden flora from the Pliocene of southern California contains an even

¹ Chaney, Carnegie Inst. Wash. Pub. No. 346, IV, p. 81, 1927.

² Chaney, Carnegie Inst. Wash. Pub. No. 349, II, p. 43, 1925.

larger number of species whose modern equivalents are now more southern in distribution. With a relative abundance of poplars, and an absence of mesic and exotic elements, the Deschutes flora represents an assemblage differing no more from other Pliocene floras of interior California and of Oklahoma than does the modern vegetation of Oregon from that in corresponding regions to the south.

No floras of Pleistocene age have been recorded in Oregon, so comparisons must be made with those described from the nearest areas to the south, in central and southern California. Even with these a comparison carries no great significance, since they are largely coastal in character. Three of the Deschutes genera, *Acer*, *Prunus* and *Salix*, are represented in the California Pleistocene, but only one of the species, *Prunus emarginata*, is similar to a Deschutes species, and it is represented by endocarps rather than by leaves. The survival of modern equivalents of all of the Deschutes species in the existing vegetation of western America may be considered to indicate that their ancestors were present at interior situations during the Pleistocene period. Whether a maple of the *negundo* type lived in eastern Oregon as late as the Pleistocene cannot be determined without a more complete fossil record. The nearest occurrence of the modern box elder to the south is in central California, nearly 500 miles distant; to the east its range in the Rocky Mountains is almost equally remote. Our present knowledge of changes in forest distribution since the Pleistocene gives us no basis for supposing that the box elder has been restricted from Oregon to central California or to the Rocky Mountain states since that time. Box elders were present in Oregon and adjacent Nevada during the Upper Miocene. They may be expected to have lingered on as relicts into the Pliocene, but the present distribution of var. *californicum* to the south, and of var. *interior* to the east, suggests that they had disappeared from eastern Oregon before the end of that epoch. The occurrence of box elders in the Deschutes formation is therefore consistent with its pre-Pleistocene age.

The physical setting of the Deschutes and the position which it occupies in the known sequence from an equable, moist climate in the Miocene to the cool, dry climate of today deserves further consideration. As above described, the rainfall at the present time is only about half that indicated by the Deschutes flora. The rainfall during the Deschutes stage is considered to have been approximately one-half that in the closing stage of the Miocene. In this trend toward aridity, determined in large part by the growth of the Cascade Range to the west, the Deschutes stage fits readily into the Pliocene epoch, and into its middle or lower portion. In like manner the floras of the Dalles and Hood River formations, on the east and west sides of the gorge of the Columbia River in northern Oregon, indicate a position in the sequence nearer to the Pliocene than to the Pleistocene. Neither of these floras has yet been described, but both of them have species in common with the Deschutes, and there is evidence that

all of them are of essentially the same age. A significant member of the Hood River flora, on the west side of the Cascades, is *Sequoia langsdorfi*, a species characteristic of the Miocene of Oregon, and not previously recorded in deposits of later age in Oregon. Its presence there indicates that this climatically sensitive tree was able to survive on the west side of the Cascade Range to a later date than on the east side, for it is absent from the Dalles and Deschutes formations. That it could have remained at this latitude, more than 200 miles beyond its present northernmost limit, as late as Pleistocene time seems wholly improbable. The relatively low temperatures which may be supposed to have prevailed in northern Oregon during the Pleistocene would have made this area even less suited to the redwood than it is today. The occurrence of *Sequoia langsdorfi* in the Hood River formation, which is contemporaneous with the Deschutes, indicates the improbability that these beds are younger than Lower to Middle Pliocene.

Such an age reference for the Deschutes formation, and the flora which it contains, appears to be consistent with other lines of evidence as to its age. In his discussion of the age of the formation,¹ Stearns has mentioned its general similarity, both in structure and lithology, to the Rattlesnake formation of the John Day Basin. The age of the latter is considered by Merriam, Stock and Moody to be Middle Pliocene on the basis of its mammalian fauna.² No plant remains have been found in it, as elsewhere discussed. A possible reason for their absence is the low altitude of the Rattlesnake site of deposition as compared with the Deschutes; greater aridity at this level would not only reduce the numbers of plants which might live there, but would render less likely their preservation. On the basis of a correlation with the "Satsop" (in this paper termed Hood River) formation of the Columbia Gorge, which was considered to be of Pleistocene age on the basis of its fossil plants,³ Stearns has considered the possibility that all or part of the Deschutes formation is referable to the Lower Pleistocene. As above indicated it is now believed by the writer that the plant fossils of the Hood River formation indicate a Pliocene rather than a Pleistocene age. In his final age reference of the Deschutes formation, Stearns states that it is to be considered of late Tertiary or early Pleistocene age. In a recent letter Stearns makes the following comment:

"I was indeed glad to learn from your letter of September 10 [1936] that you now consider the Deschutes formation Pliocene. I believed it was of this age when I described it in my bulletin but after the manuscript was submitted to Washington, Ira Williams wrote such a convincing letter to the Survey regarding correlating the Deschutes formation with the Satsop that I revised my manuscript accordingly."

¹ U. S. Geol. Surv. Water-Supply Paper 637-D, p. 142, 1931.

² Carnegie Inst. Wash. Pub. No. 347, III, pp. 58-60, 1925.

³ *Op. cit.*, p. 142.

Since Williams' opinion as to the Pleistocene age of the "Satsop" (Hood River) was based on an incorrect age determination of the flora, which is now considered to be of Pliocene age, Stearns' original idea as to the age of the Deschutes formation is consistent with the bulk of evidence that it is older than Pleistocene.

Basing his opinion on its undisturbed position and upon several other but less significant criteria, Hodge has indicated his belief that the Madras formation, including beds here termed the Deschutes formation, is of late or post-Pleistocene age.¹ More recently ² he has stated that he considers it to be of earlier Pleistocene age. These opinions, insofar as based on structural relations, are not consistent with the dating of the Rattlesnake formation in eastern Oregon, whose structure is similar. Although I have not seen the field relations at the base of the Deschutes formation, I have no question as to the reliability of Hodge's observations that it "lies unconformably upon the mature erosion surface of the Clarno, John Day and Columbia basalt formations."³ The same position is described by Merriam, Stock and Moody for the Rattlesnake formations in the John Day Basin 75 miles to the east:⁴

"Unconformably overlying the Mascall beds throughout the basin of the East Fork is an extensive series of gravels and tuffs with an intercalated bed of rhyolite, constituting the Rattlesnake formation. The Rattlesnake occasionally overlaps the Mascall and lies directly upon the basalt; from Antone to Mitchell it lies successively upon basalt, pre-Tertiary, and Clarno; on the south side of the John Day River from the 'iron bridge,' 8 miles east of Dayville, to Canyon City, it rests upon crystalline rocks of pre-Tertiary age."

The age of the Rattlesnake is definitely established as Middle Pliocene on the basis of its mammalian fauna. Since its position is essentially horizontal, it seems clear that in the John Day Basin there has been no marked orogeny subsequent to Middle Pliocene time. A similarly stable history may be supposed to have characterized the region to the west where the Deschutes formation was deposited. It is therefore not necessary to assume, as Hodge has done, the Pleistocene age of the Deschutes formation on the basis of its undisturbed position.

As a result of extensive field studies in the intervening area, Hodge has concluded that the Deschutes formation and the Dalles formation are continuous and of the same age, and that these are equivalent to at least a portion of the Hood River formation in the Columbia Gorge. The studies of Buwalda and Moore represent the most comprehensive discussion of

¹ Pan-American Geologist, vol. 49, No. 5, p. 352, 1928.

² Letter of Sept. 16, 1936.

³ *Op. cit.*, p. 351.

⁴ *Op. cit.*, p. 53.

the Dalles formation.¹ Their field work has not included the area in which the Deschutes formation is exposed; but as above stated, these formations are considered by Hodge to be equivalent, an opinion which is substantiated by the resemblance of their fossil floras. The Dalles formation is considered by Buwalda and Moore to be of Upper Miocene or Lower Pliocene age.² A similar age is assigned to the Hood River formation, which is the name given by these authors to the portion of the "Satsop" which is exposed in the Columbia Gorge region. The reasons given for this age determination are both geological and paleontological. They include correspondence in structure between the Dalles formation and the underlying basalt, the induration of the Dalles and Hood River formations, and lithologic similarity to beds such as the Ellensburg of Washington, which is considered by these authors to be of late Miocene or Lower Pliocene age. A report by Stock on the only significant mammalian fossil as yet discovered in the Dalles formation discusses the tooth of a *Hipparion*-like horse, to which he assigns an Upper Miocene or Lower Pliocene age.

The position of the Dalles and Hood River formations as described by Buwalda and Moore, and as observed by the writer, differs from that of the Deschutes formation in being folded parallel with the underlying Columbia lavas instead of lying across the upturned and eroded edges of these basalt flows. Two alternative explanations for this difference in structure may be suggested:

(1) The Dalles and Hood River formations may have been deposited before the episode of mountain making which resulted in the uplift of the Cascade Range; in this case they would be somewhat older than the Deschutes formation, which was laid down after the orogeny, as indicated by the structural unconformity at its base. The conformable position of the Dalles and Hood River formations upon the Columbia lavas was the principal basis for the statement by Buwalda and Moore that they are older than the Rattlesnake formation, which has the same stratigraphic relations as the Deschutes formation. Since the Rattlesnake is dated as Middle Pliocene by a mammalian fauna, these authors consider the Dalles and Hood River formations to be at least as old as Lower Pliocene.

(2) The folding of the Columbia lavas may have occurred at a somewhat later date in the area where the Dalles and Hood River formations occur, than in the region to the south where the Deschutes formation outcrops. Whereas the lavas had been uplifted and eroded before the deposition of the Deschutes, they may have remained in their original attitude adjacent to the Columbia River until after the deposition of the equivalent Dalles and Hood River formations.

In view of the similarity in facies of the fossil floras from the Deschutes and Dalles formations, it appears that there is no great difference in age.

¹The Dalles and Hood River Formations, and the Columbia River Gorge: *Carnegie Inst. Wash. Pub. No. 404*, II, pp. 11-26, 1 fig., 1930.

²*Ibid.*

A gap as great as from Lower to Middle Pliocene seems to me wholly reasonable, and is consistent with the first alternative. It is equally proper to assume that the floras are of the same age, in which case the second alternative must be invoked to explain the structural differences of the beds involved. Present knowledge of Pliocene floras in western America is not sufficiently complete to permit the paleobotanist to distinguish with certainty between those representing the lower and middle portions of the Pliocene.

In the judgment of the writer, the dating of the Deschutes formation as Lower to Middle Pliocene is confirmed by the following lines of evidence:

(1) The composition and climatic indication of its fossil flora, and of the related floras of the Dalles and Hood River formations.

(2) The occurrence of a *Hipparion*-like horse in the related Dalles formation.

(3) The structure and lithology of the beds as compared with other Pliocene deposits of the Columbia Plateau, notably the Middle Pliocene Rattlesnake formation of the John Day Basin.

SYSTEMATIC DESCRIPTIONS

Since all except one of the species of the Deschutes flora have previously been described from the Tertiary of western North America, the systematic portion of this paper will be brief. However, it seems desirable at this point to consider certain criteria used for establishing fossil leaf species, since the treatment of fossil vegetation is of necessity different from that of modern.

Three of the Deschutes species are distinguished from related species of the Miocene largely on the basis of their smaller size and thicker texture. *Populus plicatremuloides*, the dominant species, resembles closely the leaves of modern aspens which occupy the drier part of the range of *P. tremuloides*. This living species, growing in more humid habitats, bears leaves which are similar, in their larger size and thinner texture, to those of the Miocene species, *P. lindgreni*. Here are 2 fossil species which resemble a single living species within whose range of leaf variation both the fossils are included. The question may well be raised as to whether 2 fossil species may properly be designated under such circumstances.

In like manner, *Populus alexanderi* of the Deschutes flora appears to represent a smaller and thicker derivative of the Miocene *P. eotremuloides*. Both of these fossil species are included within the range of leaf variation of their modern equivalent, *P. trichocarpa*. *Prunus irvingi* shows a similar relationship to *P. coveus* of the Miocene, and these fossil cherries are likewise related to a single living species, *P. emarginata*. In all cases the fossil species from the Deschutes flora have a smaller size and thicker texture than related species of the Miocene; in all cases the equivalent modern species

include 2 fossil species within their range of variation, the larger and thinner-leaved types occupying a more mesic habitat than the smaller and thicker. These relationships assume significance in view of the well established trend toward lessened precipitation in western America during the Tertiary. Since the small and thick-leaved fossil species are in all cases members of the Deschutes formation, which is younger than the Miocene deposits in which the larger and thinner fossil species occur, it may be suggested that their size and texture have actual stratigraphic value in indicating post-Miocene age. One of the principal reasons for differentiating fossil species is to emphasize their time significance. It therefore seems apparent that establishing a sequence from large and thin to small and thick leaves of poplar and cherry may become highly significant in determining the age of the deposits in which they occur.

It may be suggested that since the modern equivalents show a range in leaf variation which includes the differences between corresponding fossil species, there can be no sound basis for time distinctions based upon them. To such comment it may be answered that during the Miocene, as judged by the fossil record, only the large-leaved types of aspens, cottonwoods and cherries were living near sites of deposition. If there were small and thick-leaved types, they occupied distant, more arid slopes too far from sites of deposition to enter the fossil record. It may be further stated that on the basis of the known Pliocene record, the poplars and cherries which lived near sites of deposition were entirely of small and thick-leaved type. There is expressed in this change in character of leaves, in the two latest epochs of the Tertiary, a change in physical conditions which is of fundamental significance to any understanding of the later earth history of western North America. If it be objected that these are "ecologic" species, which fall within the limits of single biologic species of today, the reply may be made that there are many plant species, both living and fossil, which are differentiated on the basis of characters far less significant.

The only apparent weakness in the method of species separation here employed is that in the case of *Prunus irvingi*, represented in our collections by only 2 specimens; the differences between it and *P. coveus* of the Miocene might be less apparent if a larger series of specimens was available for comparison. It is admitted that many of the more obvious systematic errors in paleobotany are due to inadequate fossil material, and that our separation of this Pliocene species of cherry may prove to be unjustifiable in the light of future, larger collections. But the 2 species of poplar in the Deschutes flora are represented by sufficiently numerous specimens to indicate that distinguishing specific characters of size and texture are constant in the vegetation from this horizon.

The illustrations of the Deschutes species are shown in natural size except in one case as indicated on plate 3.

***Populus pliotremuloides* Axelrod**

(Plate 6, fig. 4; plate 7, fig. 1c, d)

Populus pliotremuloides Axelrod, Carnegie Inst. Wash. Pub. No. 476, III, p. 169, pl. 4, figs. 1, 2, 3, 1937.

Leaves of this species are extremely numerous. They average 3 centimeters in length and 3.4 centimeters in width (22 measurements) as compared with 3.3×3.7 centimeters for the 3 type specimens figured by Axelrod from the Mt. Eden beds of southern California. The dimensions of our largest leaf are 4×5 centimeters, and of the smallest 1.7×2.1 centimeters. These fossil leaves are closely similar in proportion to leaves of the modern *P. tremuloides* from a dry slope in Modoc County, California. (See sheet number 71755, University of California Herbarium.)

From *P. lindgreni*, a common Upper Miocene species, our material differs in definitely thicker texture of its leaves, and their smaller size. The dimensions of 6 of the Miocene leaves average 5.4×5.7 centimeters, with none of them as small as the largest of *P. pliotremuloides*. Modern leaves of this size, as shown by sheet number 54209 in the herbarium of the University of California, come from trees which occupy the relatively humid habitat in a valley of the Sierras in Siskiyou County, California. The leaves of *P. lindgreni*, like those of aspens of the same size, were thinner than those of *P. pliotremuloides* and similar living aspens.

Whether or not these 2 fossil species represent actual biologic species is a question on which there may be differences of opinion. From the standpoint of the development of vegetation, as well as from that of stratigraphic sequence, differences in size and texture make possible a ready distinction of the Pliocene from the Miocene specimens. It seems probable that if a thousand leaves of each species were available for measurement, there might be an overlapping of dimensions in the case of a small minority. However, any mistaking of *P. lindgreni* for *P. pliotremuloides* is improbable even with a series of half a dozen leaves for comparison. Under the circumstances, there can be little question of the desirability of assigning distinct names to the aspens from the Miocene and from the Pliocene of western America.

Recent review of the smaller poplar leaves from the High Plains floras indicates that one of the specimens figured as *P. lamottei*,¹ a Pliocene ancestor of the cottonwood, should be referred to *P. pliotremuloides*. This is Type No. 39334 in the paleobotanical collection of the United States National Museum, as shown on plate 5, figure 4; it comes from the Lower Pliocene horizon at Beaver County, Oklahoma. There are 2 other leaves from the Ogallala flora whose basal nervation is even more suggestive of *P. pliotremuloides*; these leaves, which have not been figured, are from the Middle Pliocene horizon of Logan County, Kansas. The average dimensions of the 3 Ogallala specimens is 2.8×3 centimeters, less than those of leaves from the California and Oregon localities. The texture appears to be definitely thinner than that of the Deschutes specimens, but this does not represent an adequate basis for separating them. Of interest is the modern occurrence, elsewhere noted, of aspens in the sandhills of Nebraska, in association with all of the other Deschutes genera.

Collection—U. C. Mus. Pal., Paleobot, Ser., Plesiotypes Nos. 1126, 1127, 1128.

¹ Chaney and Elias, Carnegie Inst. Wash. Pub. No. 476, I, p. 35, 1936.

Populus alexanderi Dorf

(Plate 6, figs. 1, 5; plate 7, fig. 2)

Populus alexanderi Dorf, Carnegie Inst. Wash. Pub. No. 412, I, pp. 75-77, pl. 6, figs. 9-11, pl. 7, figs. 1-3, 1933.

Our material closely resembles several of the specimens of this species described by Dorf from the Pliocene of California. An examination of his types indicates the probable need of restricting this species to include only those leaves which resemble the modern *P. trichocarpa* more closely than other living species of poplar. Thus specimen No. 330, represented in figure 9 on plate 6, and specimen No. 331, represented in figure 1 on plate 7, show a closer resemblance to the living *P. fremontii* than to *P. trichocarpa*, and should probably be placed under Dorf's other Pliocene species, *P. pre-fremontii*. Although they have thicker texture, the Deschutes specimens show no marked differences from his other types of *P. alexanderi*, except that none of them reach the size of his specimen No. 327.

If limited as above suggested, *P. alexanderi* bears a marked resemblance to the Miocene species, *P. eotremuloides*, from which it differs in its smaller size, much thicker texture, and generally more slender shape. Nine leaves of *P. alexanderi* average 6.2 centimeters in length and 4.3 centimeters wide. The dimensions of 8 specimens of *P. eotremuloides* average 7.2×4.6 centimeters. It is significant to note that the only Pliocene specimen (No. 327) which reaches the size of *P. eotremuloides* is from northwestern California where the comparatively humid conditions of the Miocene may be considered to have persisted longer than to the south and inland.

The significance of size in the distribution of the modern black cottonwood may be emphasized by a comparison of leaves from trees growing in humid and dry situations. Sheet No. 176664 in the herbarium of the University of California, from a moist habitat in Humboldt County, shows leaves similar in size and shape to those of *P. eotremuloides*. Sheet No. 144127, from a canyon head in the San Bernardino Mountains of southern California, shows leaves which closely resemble those of *P. alexanderi*. It is possible to conclude that with lessened precipitation from Miocene to Pliocene time in the Columbia Plateau, there was a reduction in size and an increase in thickness of the leaves of those cottonwoods ancestral to the modern *P. trichocarpa*. A similar trend in size and texture has been noted for other species of the Deschutes flora.

Collection—U. C. Mus. Pal., Paleobot. Ser., Plesiotypes Nos. 1123, 1124, 1125.

Salix florissanti Knowlton & Cockerell

(Plate 6, fig. 3)

Salix florissanti Knowlton & Cockerell, U. S. Geol. Surv. Bull. 696, p. 566, 1919.

Berry, U. S. Geol. Surv. Prof. Paper 154-H, p. 242, pl. 64, fig. 16, 1929.

Salix amygdalifolia Lesquereux, Rept. U. S. Geol. Surv. Terr., vol. 8, p. 156, pl. 31, figs. 1, 2, 1883.*Salix dryani* Knowlton, U. S. Geol. Surv. Prof. Paper 140-A, p. 33, pl. 12, fig. 6, 1926.

Since leaves of *Salix* do not in most cases furnish characters useful in specific differentiation, some danger of inaccuracy may be involved in assigning the same specific name to specimens from widely different localities. Lacking any basis for separating them, however, I am following the practice of assuming that the Miocene willows originally described from the Florissant of Colorado represent the same species as those from the Mascall of Oregon and the Latah of Washington.

Leaves of this species are less numerous than might be expected in view of the present distribution of willows in association with aspens along streams in eastern Oregon. There is no satisfactory basis for distinguishing the *Deschutes* leaves from those recorded from the Miocene of eastern Oregon, nor from those of the modern *S. caudata* which occupies stream borders in the mountains a few miles from the fossil locality. Paleobotanical practice does not encourage the use of the name of a living species for these fossils, but it seems wise to apply the Miocene name to our Pliocene specimens. It seems clear that these specimens offer little stratigraphic evidence in view of their resemblance to older and to younger willows.

Collection—U. C. Mus. Pal., Paleobot. Ser., Plesiotype No. 1129.

Prunus irvingi n. sp.

(Plate 7, figs. 3, 4)

Description—Leaves ovate, rounded at the base and at the slightly narrowed apex; length 3.3 cm., width 1.8 cm.; midrib slender; secondaries slender, closely spaced, the lower pair tending to extend along the margin, others diverging at angles of 45 to 50°, camptodrome; tertiaries forming a coarse network, in some instances branching from the midrib between the secondaries; margin obscurely serrate; texture thick.

As elsewhere indicated, these leaves are smaller and thicker than those described from the Lower Miocene of eastern Oregon under the name of *P. coveus*. Both of the fossil species show a resemblance to the living *P. emarginata*, but the *Deschutes* leaves have a size and texture similar to those of shrubs occupying the more arid portion of its range.

P. irvingi is named in honor of Mr. Lewis H. Irving of Madras, who has long been interested in the Tertiary paleontology of eastern Oregon, and who is responsible for the discovery of many of the specimens here described.

Collection—U. C. Mus. Pal., Paleobot. Ser., Cotypes Nos. 1130, 1131.

Acer negundoides MacGinitie

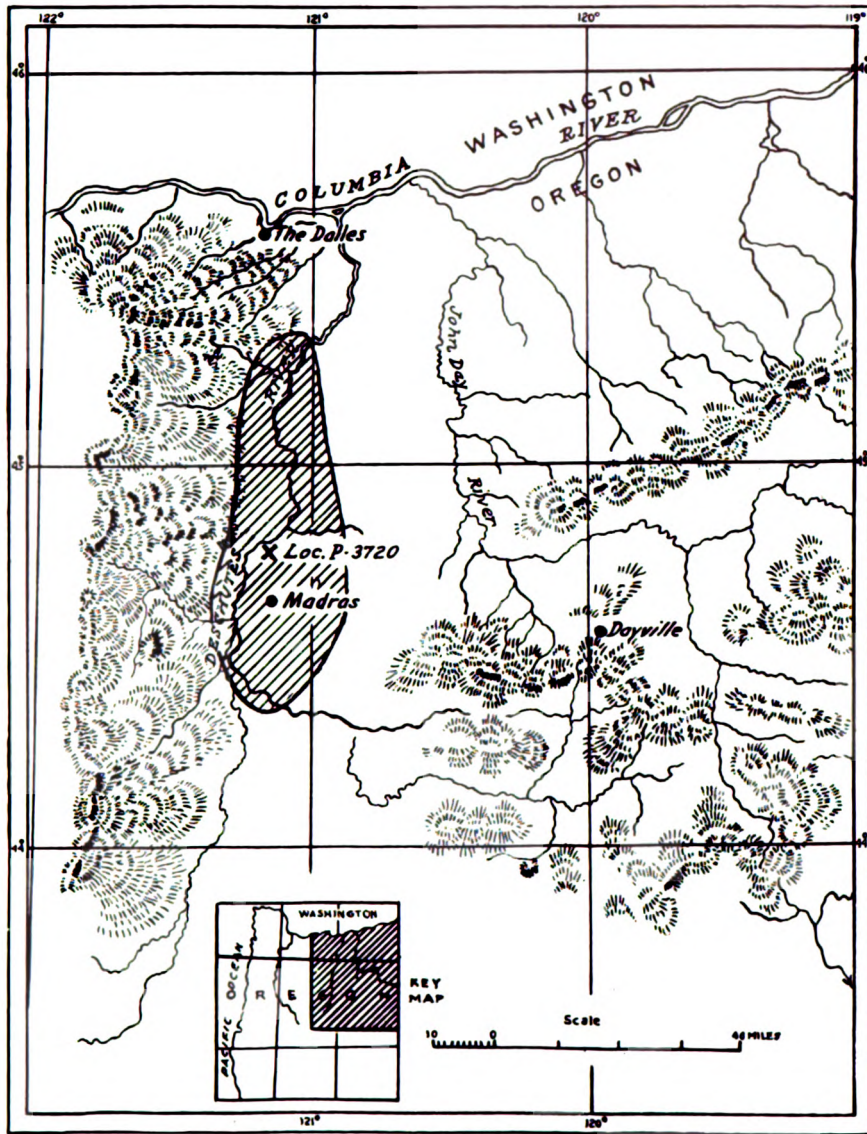
(Plate 6, fig. 2; plate 7, figs. 1a, b)

Acer negundoides MacGinitie, Carnegie Inst. Wash. Pub. No. 416, II, p. 62, pl. 11, figs. 2, 3, 1933.

This species was originally described from the Upper Miocene Trout Creek flora of southeastern Oregon, on the basis of winged fruits. Up to the present time, little has been known of the leaves, although single fragmentary specimens associated with fruits have been recorded from the Upper Miocene of 49 Camp, Nevada, and from a Lower Pliocene horizon in the Ogallala formation of Beaver County, Oklahoma. In the *Deschutes* formation, and to an even greater extent in the Dalles beds to the north, there are abundant box elder leaflets as well as fruits. A description of the foliage will be included in a forthcoming paper on the flora of the Dalles beds.

Since there is no basis for distinguishing the seeds collected at these widely scattered localities, it seems proper to refer them all to one species. Possibly future collections of leaves or other structures may reveal differences of a sort used for separating such varieties as *californicum* and *interior* in the modern vegetation over a comparable area.

Collection—U. C. Mus. Pal., Paleobot. Ser., Plesiotypes Nos. 1132, 1133, 1134.



Map of North Central Oregon showing the approximate distribution of the Deschutes formation (shaded area).

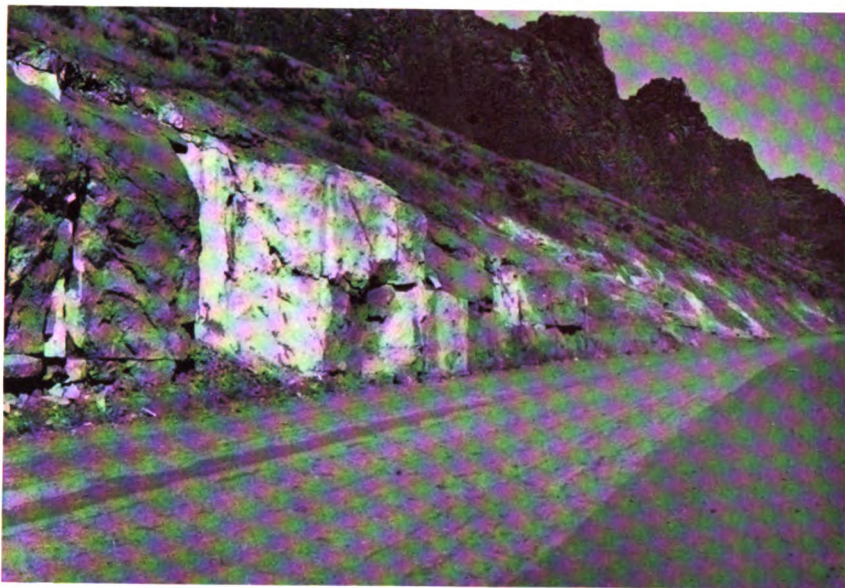


FIG. 1—Locality P3720, showing the mudflow at the base of which the leaves of the Deschutes flora were collected. Molds of several trees are shown by vertical lines on the face of the cut.



FIG. 2—Boulder slide that came down Mageik Canyon from slopes of Mount Katmai and spread over the floor of Katmai Valley. (Photograph by C. N. Fenner.)

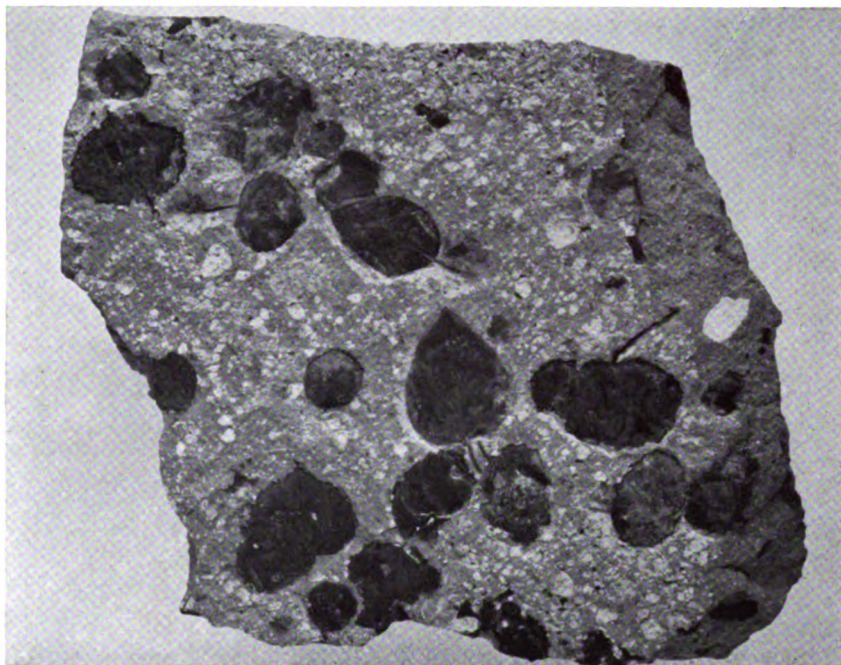


FIG. 1—Detail of slab shown in figure 2, showing leaves of *Populus alexanderi* and *P. pliotremuloides*. $\times 1/3$.

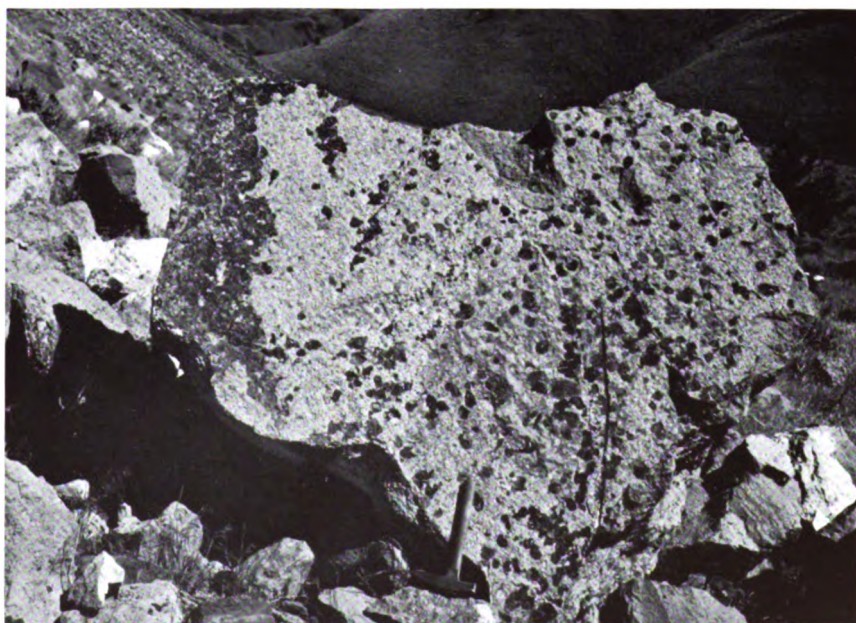


FIG. 2—Slab of pumiceous tuff from the base of a mudflow in the Deschutes formation. This has been thrown down the slope below the roadcut during highway construction.



FIG. 1—Cross section of a core taken from the ash deposit in Silver Lake, 10 feet from the shore. This represents a concentration of spruce needles about 5 inches above the base.

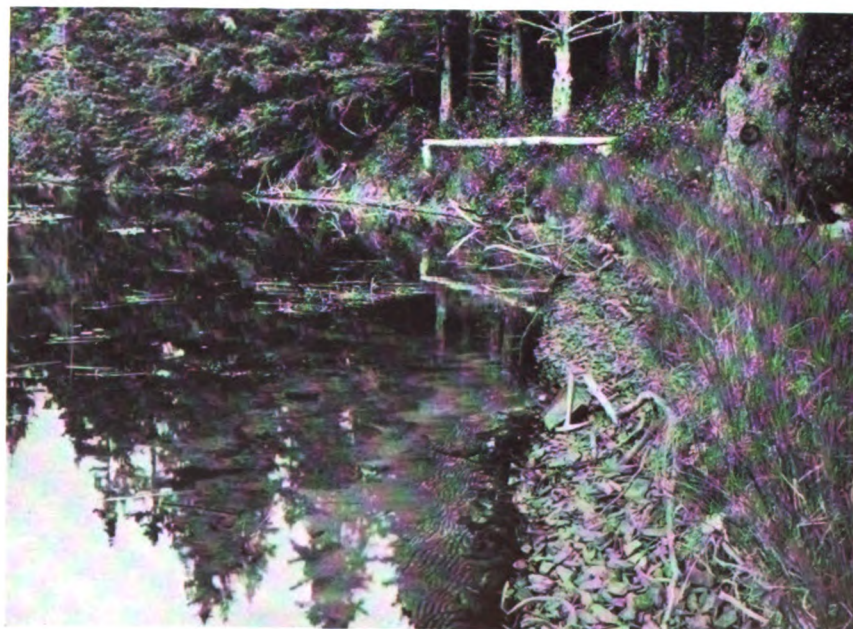


FIG. 2—Silver Lake at the point where cores were taken, showing ripple-marked ash along the shore.

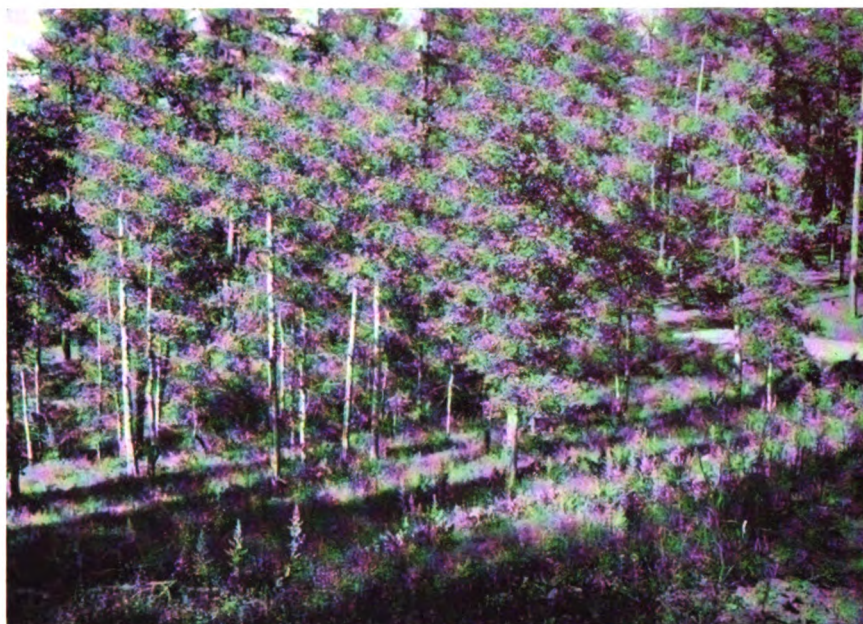


FIG. 1—Aspens in the yellow pine forest on the south slope of the Ochoco Mountains at an altitude of 5000 feet.



FIG. 2—Aspens associated with black cottonwood, cherry, willow, and several other types of woody plants on the borders of a small stream in the Blue Mountains near Mitchell, at an altitude of 3400 feet.

PLATE 6

- FIGS. 1, 5**—*Populus alexanderi* Dorf. Plesiotypes. U. C. Mus. Paleontology, Paleobot Ser. Nos. 1123, 1124.
- FIG. 2** *Acer negundooides* MacGinitie. Plesiotype. U. C. Mus. Paleontology, Paleobot, Ser. No. 1132.
- FIG. 3**—*Salix florissanti* Knowlton and Cockerell. Plesiotype. U. C. Mus. Paleontology, Paleobot, Ser. No. 1129.
- FIG. 4**—*Populus pliotremuloides* Axelrod. Plesiotype. U. C. Mus. Paleontology, Paleobot, Ser. No. 1126.



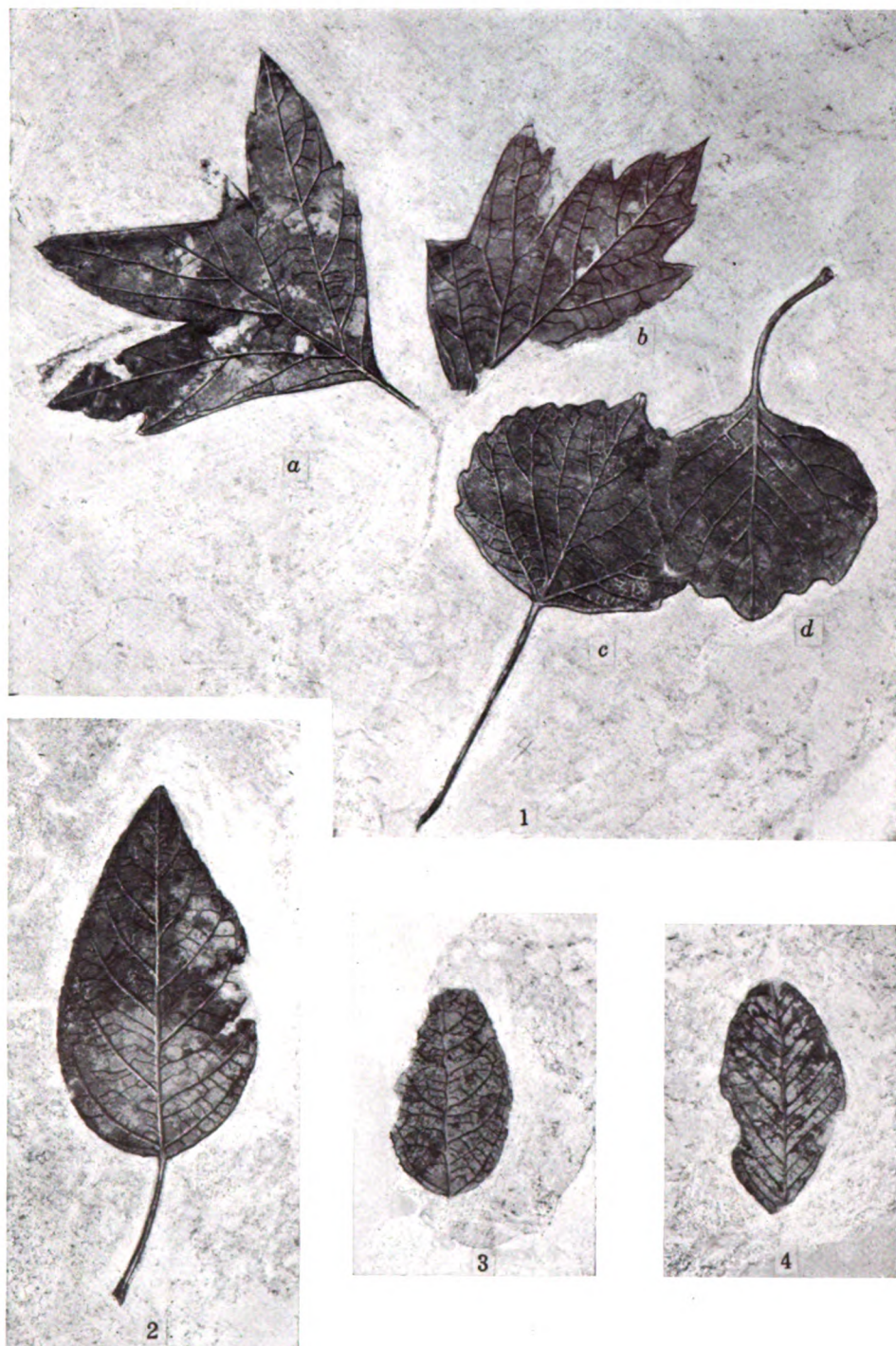
PLATE 7

FIG. 1a, b—*Acer negundoides* MacGinitie. Plesiotypes. U. C. Mus. Paleontology, Paleobot. Ser. Nos. 1133, 1134.

FIG. 1c, d—*Populus pliotremuloides* Axelrod. Plesiotypes. U. C. Mus. Paleontology, Paleobot. Ser. Nos. 1127, 1128.

FIG. 2—*Populus alexanderi* Dorf. Plesiotype. U. C. Mus. Paleontology, Paleobot. Ser. No. 1125.

FIGS. 3, 4—*Prunus irringi* Chaney. Cotypes. U. C. Mus. Paleontology, Paleobot. Ser. Nos. 1130, 1131.



CONTRIBUTIONS TO PALÆONTOLOGY

V

THE SAN PABLO FLORA OF WEST CENTRAL
CALIFORNIA

BY CARLTON CONDIT
University of California

With seven plates and one text-figure

[Issued April 21, 1938]

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THE SAN PABLO FLORA OF WEST CENTRAL CALIFORNIA

INTRODUCTION

The first known collections of leaf impressions from the San Pablo beds of middle California were made by Professor J. D. Whitney of the University of California in the early eighties of the last century. Since that time collections have been made intermittently, and in the past several years they have been greatly augmented in connection with my studies of Tertiary vegetation in central California. The material described in this paper has all been secured from the region of Mount Diablo and in the hills to the south. Although the preservation is often poor, owing to coarse matrix and close jointing, it is believed that enough specimens are now at hand to permit an accurate interpretation of the fossil leaves. The San Pablo flora is of stratigraphic interest because it is contained in beds whose age has long been a subject of controversy among geologists and paleontologists. It throws important light on the physical history of California since it represents the last known flora before the initiation of typical dry summer conditions, which have persisted in this region from the Pliocene to the present.

I wish to express here my appreciation for all the assistance that I have received in this study. Many individuals have contributed specimens, and many others criticisms and suggestions. It is impossible to thank them all individually, but special acknowledgment should be rendered to Dr. R. W. Chaney, of the Carnegie Institution of Washington and the University of California, whose instruction and criticism have made this study possible; to Dr. B. L. Clark of the University of California, who has abundantly given his advice concerning the stratigraphy and paleontology; to various individuals mentioned in the body of this paper in connection with particular questions; and to the Carnegie Institution of Washington for financial aid. Dr. Mark L. Emerson of Oakland, California, has contributed some excellent specimens that he collected from Locality 618.

Many individuals have published results of studies of the San Pablo beds, the majority concerned with geology and invertebrate paleontology of these sediments, of which the papers by Clark¹ are the most comprehensive. There are only four papers dealing with the fossil flora. In 1883 Lesquereux² reported upon some leaves from the San Pablo of Corral Hollow and Contra Costa County. He determined their age to be Miocene.

¹ Clark, B. L., *The Neocene Section at Kirker Pass on the North Side of Mount Diablo*, Univ. Calif. Pub. Geol., vol. 7, No. 4, pp. 47-60, 1912; *The Fauna of the San Pablo Group of Middle California*, Univ. Calif. Pub. Geol., vol. 8, No. 22, pp. 385-572, 1915.

² Lesquereux, L., *U. S. Geol. Surv. Terr. Rept.*, vol. 8, pt. 3.

Some of his type specimens are in the Museum of Paleontology of the University of California, where I have been able to examine them. In some cases, I have revised his determinations in the light of the increased knowledge of fossil plants now available. These revisions are included in the systematic portion of this paper.

In 1889 Lesquereux¹ reported upon some leaves collected by Turner from Kirker Pass (Loma Ranch), and listed several species which have not been found since, in addition to others that are common in my collections. I have not seen the specimens, and do not feel justified in including them in the discussion of the flora, because their relationships are indeterminable on the basis of published drawings. These species are *Diospyros virginiana* Linné, var. *turneri* Lesqx.; *Viburnum* cf. *rugosus* Pers.; and *Vitis* sp. Assuming that they are correctly identified, none of these plants is out of place in association with the San Pablo flora. A small collection at the United States National Museum collected by H. W. Turner "north of Mt. Diablo" has the characteristic San Pablo lithology. It includes a large leaf of *Tetracera castaneæfolia* MacGinitie.

In 1911 Knowlton² included a list of species from Corral Hollow and Contra Costa County in his discussion of the flora of the auriferous gravels of California. None of his specimens are available to me for study, so I have not attempted any revisions of his determinations. Criticizing identifications on the basis of illustrations is not usually warrantable, but I feel sure that Knowlton, following the practice of his day, unjustifiably multiplied species, and even genera. For instance, he lists 8 leaf species of *Laurus* and *Persea*, including 4 that had been previously determined by Lesquereux. All of these are included within the range of leaf variation of the modern *Persea borbonia*, which, like many lauraceous species, exhibits a great variety of leaf shapes. Furthermore, it is extremely unlikely that eight lauraceous species with similar leaves ever grew together in a temperate climate. These considerations have led me to record but one species of *Persea*, but to withhold formal synonymy until I have an opportunity to examine the type specimens of Knowlton's species. Included in the list in this paper is *Ficus asimineæfolia* Lesqx., supposedly occurring in the Corral Hollow collections. But Lesquereux described it from a locality he called "Rock Corral, Placer County, California" in volume 8 of the U. S. Geol. Surv. Terr. Rept., and Knowlton himself in his 1919 *Catalogue of the Mesozoic and Cenozoic Plants of North America* does not list it as occurring at Corral Hollow. The specimens are not in Lesquereux's collections at the University of California. These considerations suggest that its inclusion in the Corral Hollow list in this paper was an error. According to the figures published, it does not closely resemble the figs that occur in Florida today; if it did, its presence in the flora would excite no comment. If it is related

¹ Lesquereux, L., U. S. Nat. Mus. Proc., vol. 11, p. 35, 1889.

² Knowlton, F. H., U. S. Geol. Surv. Prof. Paper 73, pp. 57-64, 1911.

to figs with a more tropical distribution, its acceptance in the flora is open to serious doubt, and must be withheld until all confusion concerning its locality is removed. This is the safer procedure, even though another tropical genus (*Tetracera*) appears to be present in the San Pablo beds.

In 1926 Flora Murray Scott¹ reported upon a small collection of leaf impressions from the San Pablo of the Tesla region. She applied names of modern California species to the fossils. In most cases the fossil leaves of the San Pablo do resemble the species to which she referred them, but bear closer resemblances to eastern species of the same genera. The present practice in paleobotany is to give different names to fossil species, even though they may closely approach modern species.

All of the fossil localities occur along the eastern edge of the Coast Ranges, which in this region are little more than moderately high hills. The highest point, Mount Diablo, which lies between the northern and southern localities, attains an elevation of 3849 feet. The remainder of the range scarcely reaches elevations of 1000 feet. In this region the coast line and the main trend of the ridges is northwest-southeast, with the isotherms and the isohyets paralleling them. The Coast Ranges in general are humid, but according to Russell,² border on arid regions. The fossil localities are considerably drier than the western portion of the hills. On the basis of records from 1901 to 1920, Russell has determined that the region suffers dry years less than half the time.³ He defines a dry year by a ratio between mean annual temperature and the annual precipitation. According to climatic maps of the region the rainfall varies between 15 and 17 inches yearly, increasing toward the coast and decreasing inland. Almost all of this rain falls in the winter and spring, with a long dry season in the summer and autumn.

The mean annual temperature is approximately 57° or 58° Fahrenheit. The temperature decreases toward the coast and increases inland across the Great Valley, decreasing again up the slope of the Sierra. The hottest days occur in July or August and the coldest in January. The season between the last killing frost of each winter and the first of the next winter runs about 290 or 300 days, although temperatures below 32 degrees Fahrenheit occur both before and after the limits of the killing frosts. Strong westerly winds are frequent in the region especially in the summer months. These, although directly from the sea, have been warmed by contact with the hot dry hills, and probably intensify the dry season by increasing evaporation from the eastern portion of the Coast Ranges. These data are summarized from the reports of the United States Weather Bureau. From them it is apparent that the chief factor in the climatic effect upon the vegetation of the region is moisture rather than temperature relations.

¹ Scott, F. M., Bull. Torr. Bot. Club, vol. 53, No. 6, pp. 403-409, 1926.

² Russell, R. J., Dry Climates of the United States, I, Univ. Calif. Pub. Geog., vol 5, No. 1, 1931.

³ *Ibid.*, II, Univ. Calif. Pub. Geog., vol. 5, No. 5, 1932.

The vegetation shows clearly a response to these conditions. Grassland is the dominant climax, mostly composed of naturalized wild oat (*Avena fatua* L.). Trees occur irregularly along stream courses, and are prominent only in canyons that contain permanent streams. At Loma Ranch only a few individuals occur, some in stream bottoms and some scattered on the slopes. *Quercus agrifolia* Nee, *Q. lobata* Nee, *Æsculus californica* Nutt., and *Photinia arbutifolia* Lindl. have been noted. At Altamont Pass no trees are present. This locality is farther east and even drier than the other localities. In Corral Hollow *Populus fremontii* Wats., *Platanus racemosa* Nutt., *Salix* sp. occupy stream bottoms with *Juniperus californica* Carr. and oaks on the hillsides. On the protected north slope of Mount Diablo at elevations that receive more rain, a fairly well developed digger pine forest occurs. In Franklin Canyon, several miles west of Loma Ranch, several more mesic species occur along a stream that flows in all but the driest years. *Salix*, *Umbellularia californica* Nutt., *Æsculus californica*, *Quercus agrifolia*, *Platanus racemosa*, *Acer macrophyllum* Pursh., and a walnut that may not be native are abundant. Near the city of Oakland, in the westernmost part of the hills, a deep canyon supports *Sequoia sempervirens* Endl. and some of its associates. These various localities illustrate the increasing dryness from west to east in this region. All of the area has been affected by man, and the present vegetation may not represent the natural reaction to the climate. For instance, Loma Ranch is used for sheep grazing during the spring months, which may have a deterrent effect upon the establishment of tree seedlings. However, comparisons with other areas nearby which are ungrazed gives no indication that the natural vegetation was different from the one now found there.

GEOLOGIC RELATIONS

The brief statement of the geology of the San Pablo Group that follows has been taken largely from the work of Dr. B. L. Clark,¹ amplified by later studies and some of the writer's observations.

The San Pablo Group or beds equivalent to it are distributed along the Coast Ranges from a short distance north of San Francisco Bay southward to the vicinity of Santa Barbara, California. It has not been recognized in the Great Valley or on the slopes of the Sierra Nevada. Louderback² has suggested that the San Pablo represents the marine equivalent of the andesitic fluviatile deposits locally distributed on the western flank of the Sierra. Williams³ has pointed out the lithological resemblances of the upper part of the Sutter formation at Marysville Buttes to both the Sierra andesites and the San Pablo, and has suggested that they may all be the same age.

¹ Clark, B. L., *op. cit.*

² Louderback, G. D., Period of Scarp Production in the Great Basin, Univ. Calif. Pub. Geol., vol. 15, No. 1, pp. 1-44, 1924.

³ Williams, H., Geology of the Marysville Buttes, California, Univ. Calif. Pub. Geol., vol. 18, No. 5, pp. 103-220, 1929.

The relations of these sediments will be discussed in later papers concerning the floras that are contained in the fluviatile sediments of the Sierra.

The type section of the San Pablo is located on the eastern shore of San Francisco Bay near the town of Rodeo. Here the sediments are considered to be wholly marine, with a thickness of about 2200 feet. They are exposed in a syncline whose axis strikes northwest into the bay. Originally considered as one formation, the San Pablo was divided into two formations by Clark¹ in 1912. The lower was subsequently named the Cierbo and the upper the Neroly. In 1922 Trask² added the underlying Briones

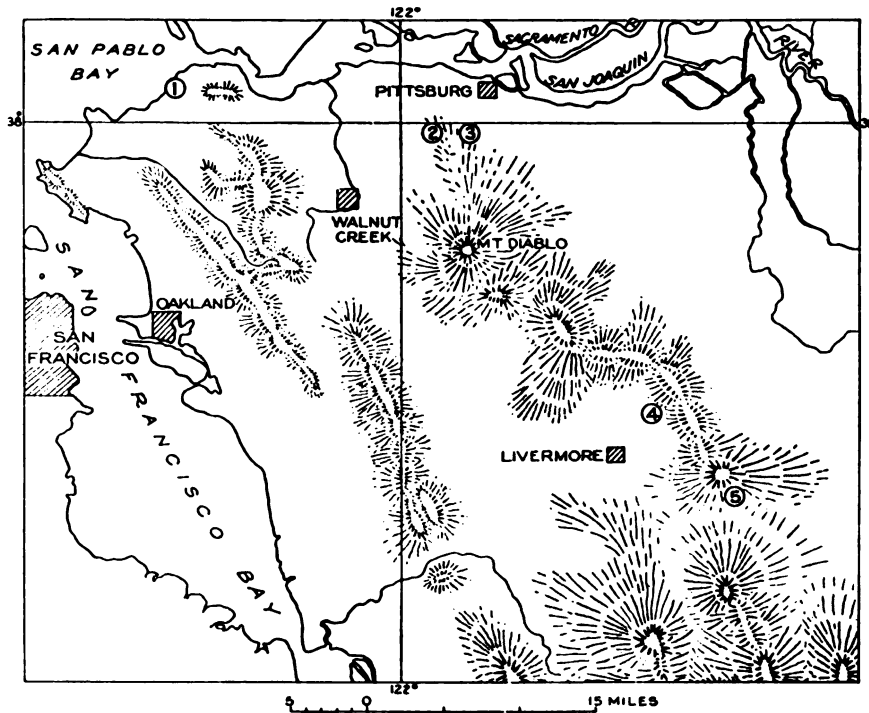


FIG. 1—Map of the area in which the San Pablo flora is found:

- | | |
|------------------------------------|---------------------------------|
| 1. Type section of San Pablo Group | 4. Locality 199, Altamont Pass |
| 2. Locality 618, Bailey Road | 5. Locality P361, Corral Hollow |
| 3. Locality 607, Loma Ranch | |

formation to the San Pablo Group on structural and invertebrate faunal evidence. This supported a statement by Clark³ in 1915 that the Briones may have had a closer relationship to the San Pablo than to the underlying Monterey. At the present time, then, the San Pablo is considered to consist of three formations, named, from the base up, the Briones, the Cierbo, and the Neroly. All three formations are rarely present in the same section. Below the Briones, or whatever formation of

¹ Clark, B. L., Univ. Calif. Pub. Geol., vol. 7, No. 4, pp. 47-60, 1912.

² Trask, P. D., The Briones Formation of Middle California, Univ. Calif. Pub. Geol., vol. 13, No. 5, pp. 133-174, 1922.

³ Clark, B. L., Univ. Calif. Pub. Geol., vol. 8, No. 22, pp. 385-572, 1915.

the group happens to be lowest, are middle Miocene or older sediments, separated from the San Pablo by an unconformity. Above the Neroly, sometimes unconformably and sometimes apparently conformably are locally the Pinole tuff, the Orinda formation, and the Merced formation, all of Lower Pliocene age. There are indications of minor unconformities between the various members of the San Pablo Group.

Studies now in progress indicate the presence of another formation above the Neroly and below the Orinda in the vicinity of the Mount Diablo Country Club, on the southwest side of the mountain. Close to what is considered to be the contact between the Neroly and the new formation are abundant poorly preserved leaf impressions of typical San Pablo species. This new formation has been tentatively named the Alamo formation.

All the leaves discussed in this paper have been taken from the Neroly formation. Leaves are abundant in many places but usually are not well preserved. The following four localities have furnished the majority of the specimens studied. Table 1, page 232, lists the species found and their relative abundance at each locality.

Locality 607—Loma Ranch, Contra Costa County, California is in the center and northwest quarter of Section 30, Township 2 North, Range 1 East, Mount Diablo Baseline and Meridian. Loma Ranch lies in the northeast portion of the hills south of Pittsburg, on the Donovan Road, which connects that town with the Marsh Creek Road. In this area the upper member lies parallel to the hills, striking northwest and dipping to the northeast about twenty-five degrees. It extends along the innermost ridge for a distance of several miles. It is composed of blue-gray sand, white, buff, and gray shale, and occasional small lenses of conglomerate. All is considerably mixed with andesitic tuff, especially near the top. In some places the conglomerate is so minor that it amounts to no more than lines of small rounded pebbles separated horizontally from each other by a distance of several inches, the intervening area filled with andesitic sand. The leaf-bearing beds are crossbedded, and the alternate layers of sand and shale are not continuous over long distances. The sand layers are more resistant than the finer-grained beds, so that erosion has carved the formation into a series of small cliffs and ledges separated by grass-covered slopes.

Leaf impressions are common in many places in this area. Almost every fine-grained layer reveals traces of plant remains, and many of the coarser ones also. One of the best exposures is in a stream bottom about a mile northwest of Donovan Road. Here the action of the stream has exposed a bed of coarse sand capping a layer of tuff about two and a half feet thick. These lie on the south bank, and dip into the stream bed. The same beds occur farther up the stream, on both banks, which here parallels the strike of the beds. Leaves are abundant in the tuff. About an eighth of a mile upstream from this place a silicified stump is stratigraphically close to the leaf layer, and is standing normal to the bedding planes. Several root-like

masses of petrified wood are also exposed along the strike of this bed within a distance of a few hundred yards in either direction.

Less than a quarter of a mile southwest of this exposure a long low escarpment of sandstone outcrops on one side of a draw leading up to a small saddle between two hills. This is exposed along a line running southeast. Immediately below the sandstone is a bed of tuff that contains abundant leaves. Some leaves also occur in the sandstone. About three-quarters of a mile from the road a prospect shaft has been sunk into the beds, going down about with the dip. A few years ago the hanging wall of this shaft was thickly covered with impressions of *Platanus*. Weathering has now largely destroyed these impressions. About a quarter of a mile from the road, at about the same stratigraphic level as the prospect shaft, is an exposure of leaf impressions in an overhanging cliff face.

Between this last exposure and the prospect shaft a section of the Neroly was measured with a surveyor's tape and a Brunton compass. This falls in the northwest quarter of southeast quarter of Section 30, Township 2 North, Range 1 East, Mount Diablo Baseline and Meridian. The section as measured follows:

Pinole tuff

Irregular contact

- | | |
|---|-----------|
| 21. Coarse, even-textured, friable blue sandstone. Grains well rounded, coated with blue opal, a lens of conglomerate pebbles one to two inches diameter of volcanics. The pebbles are scattered, often with several inches of sand between them..... | 18.3 feet |
| 20. Finer gray-blue sandstone, with small sharp crossbedding.. | 1.7 |
| 19. Fine-grained gray tuff, evenly bedded, containing abundant remains of roots, twigs, and macerated leaves..... | 0.9 |
| 18. Blue sandstone interbedded with gray tuff layers up to 6 inches thick | 7.9 |
| 17. Light gray to buff very fine tuff, silicified until it approaches chert in character, with abundant leaf impressions..... | 2.6 |
| 16. Fine-grained light gray friable sandstone, alternating with fine tuff layers from one-eighth to one-half inch thick. Very fine crossbedding, and scattered leaf impressions..... | 3.7 |
| 15. Coarse blue friable sandstone, as above but with no conglomerate. Crossbedding with foreset beds up to two feet in length | 13.8 |
| 14. Alternate layers of blue sand and gray sandy tuff up to two inches thick | 7.7 |
| 13. Light gray moderately coarse sand mixed with tuff. Obscurely but evenly bedded. Molds of marine mollusks and macerated plant remains common | 19.1 |
| 12. Coarse blue friable sandstone, as above..... | 8.6 |
| 11. Fine gray sandy tuff with macerated plant remains..... | 1.8 |
| 10. Coarse blue massive sandstone, crossbedded, with occasional lenses of conglomerate and scattered pebbles which are up to two inches diameter and usually well rounded, rarely sub-angular | 31.8 |

9. Coarse blue sand with layers of white or light gray fine tuff about six inches wide. The fine-grained layers contain scattered leaves and other plant remains..... 4.3 feet
 8. Coarse blue sandstone, poorly bedded..... 2.8
 7. Coarse blue sand with alternating beds of light gray tuff. Leaf impressions occur in both coarse and fine layers..... 9.2
 6. Coarse blue sandstone, poorly bedded..... 18.4
 5. White friable sandy tuff, mottled yellow, red, and brown by iron oxide, with molds of marine mollusks common..... 25.8
 4. Gray-white slightly sandy tuff with abundant molds of marine mollusks 9.8
 3. Natural terrace with thick soil cover upon underlying rocks. Judging by smaller soil-covered terraces in the section fine-grained material underlies this one. In a gully 150 feet east of the line of this section, a layer of yellow-gray sandstone containing abundant shells of marine mollusks was exposed about 23 feet below the gray-white tuff. This is continuous across the line of the section, since fragments of the rock and shells appear in the float below this level..... 66.7
 2. Yellow-gray sandy tuff..... 14.7
 1. Gray-blue sand with tuff lenses and finer sand lenses in the lower part. Plant remains occur in the finer beds..... 32.9
- Apparently conformable contact
Cierbo formation

 302.5 feet

Locality 618—Bailey Road, Contra Costa County, California. This locality is in the northwest quarter of Section 23, Township 2 North, Range 1 West, Mount Diablo Baseline and Meridian. Bailey Road follows a route over the hills from the Marsh Creek Road to the Pittsburg-Martinez Highway parallel to and about 2.5 miles northwest of Donovan Road. The Neroly formation is exposed in a roadcut about 1.5 miles from the junction of Bailey Road with the Pittsburg-Martinez Highway. Leaves occur in a fine layer in this exposure, and appear to be stratigraphically higher than the best collecting levels at Loma Ranch. Since the Neroly is continuous between here and Locality 607, and in view of the general similarity of the beds along the strike, they may be discussed together. Several differences in lithology between the two localities may be noted. At the Bailey Road locality the sediments show less marked crossbedding, and more regularly consist of gray sand and sandy tuff. At the Loma Ranch locality coarse blue sand and thin lenses of shale and tuff are more characteristic.

The fluctuation from marine to continental conditions, as indicated by the alternate occurrence of leaves and marine invertebrates, suggests deposition in a region of rapidly changing shorelines. The fact that the invertebrate fauna includes brackish-water mollusks indicates that the sediments were deposited close to shore. Abundant crossbedding indicates that deposition was rapid. The fact that the crossbedding is almost all on a

small scale suggests that the contributing streams were small. The rapid variation laterally of sediments indicates numerous small streams. The general absence of large fragments supports this; the conglomerates in the Neroly are all fine-textured and of no great extent. The conditions of sedimentation that best fit the conditions indicated are those that would occur in a region where a large stream was debouching into a sea, and dividing into a number of small distributory streams, or where a large number of small streams emptied into the basin. Since the conditions indicated are about the same at the top as at the bottom of the formation, there must have been several hundred feet of subsidence during the time the Neroly was laid down. Under these conditions one can picture a region of pools, lagoons, sandbars, and spits, the pools and lagoons sometimes salt and perhaps sometimes fresh, depending on the relations of their fresh-water and marine connections. The land areas were in part forest-covered, with trees growing so close to the shore that stumps occur *in situ* in the sediments. These conditions are similar to those in regions where the modern equivalent of the San Pablo flora is growing.

The San Pablo is separated by unconformities from the Oligocene Kirker tuff below and the Pliocene Pinole tuff above in this region.

Locality 199—Altamont Pass, Alameda County, California lies in the west center of Section 31, Township 2 South, Range 3 East, Mount Diablo Baseline and Meridian. Fossil leaves occur in a cut on the Western Pacific Railroad about 1000 feet south of a viaduct that carries the Western Pacific tracks across the Southern Pacific Railroad and the Livermore-Tracy Highway. The material is interbedded sand and clays, slightly crossbedded and closely jointed. The sand is yellow-brown to light gray, friable, moderately fine-grained, with the grains well rounded. The clay or tuff lenses are gray-brown to light gray or almost white, compact, generally harder than the sandstone, with conchoidal fracture. Leaves occur in both matrices. There is a general northwest strike, with a dip of about 25 degrees to the southwest. The hills in this region are low and rounded with a thick soil mantle, so that no natural outcrops occur. This locality occurs in a small block of Neroly that has been dropped by faulting into the Cierbo. It is not continuous with any other known Neroly. Arthur Huey,¹ who has studied the area as part of his graduate studies at the University of California, states that, on the basis of lithology, it is unquestionably Neroly. The evidence of the flora contained completely supports this determination, and no evidence is known that tends to refute it. Cierbo appears in the cuts both north and south of this locality. An interesting character of the leaf impressions collected at this locality is the large number of them that are twisted, folded, or curled. The proportion of such leaves is high in contrast with the other localities. Curled leaves are usually taken to indicate subaerial deposition, since subaqueous deposition tends to soften and

¹ Huey, A., written communication, June 3, 1936.

flatten them out. The seven species that are abundant or common at this locality are all of the type that grow along stream borders. The irregular alternation of sand and tuff, and the mingling of the two that often occurs, may indicate that this was a bar or bank that was periodically dry, receiving æolian deposits for at least part of the time. Such dry bars are not uncommon in regions of delta-like deposition along the lower portions of stream courses.

Locality P361—Corral Hollow, Alameda and San Joaquin Counties, California is in the northeast quarter of northwest quarter of Section 29, Township 3 South, Range 4 East, Mount Diablo Baseline and Meridian. Poorly preserved leaves in a closely jointed matrix are found 1.25 miles north of the Tesla Road, in a creek bottom that crosses the road at the Alameda-San Joaquin County line a short distance east of Benchmark 699. Leaves have also been found in several other places on the north side of Corral Hollow. Most of them occur in a gray tuffaceous shale that lies immediately below the blue sandstone member. Leaves are occasionally found also in the sandstone. Here the San Pablo consists of Cierbo resting with a profound unconformity upon Cretaceous Panoche, and Neroly overlying with slight angular unconformity. Above the Neroly is the Pliocene Alamo formation, separated from it by a slight unconformity. On the north side of Corral Hollow the structure is considerably complicated by folding and faulting, with the attitude of the San Pablo changing rapidly from place to place. At the locality described the San Pablo dips south to form a dip slope although east and west of this place its dip is reversed. In the hills north of Corral Hollow San Pablo outcrops in many places, often showing sharp small folds. In this area the San Pablo is no more than 300 feet thick, with the Neroly making up as little as 50 feet of that thickness in some places, and nowhere amounting to more than 100 feet.

The bottom of Corral Hollow marks the trace of an important fault, with the south side upthrown, exposing Eocene beds on the south side of the canyon. No San Pablo occurs for several miles south of the Hollow. I have collected leaves from the south center of Section 17, Township 4 South, Range 4 East, Mount Diablo Baseline and Meridian, which is more than 3 miles south of Corral Hollow. Here the exposure is typical Neroly, and the leaves, although neither abundant nor well preserved, include such typical and easily recognized San Pablo species as *Persea princeps*, *Platanus dissecta*, *Populus balsamoides*, *Prunus chaneyi*, and *Taxodium dubium*. Lesquereux's collection includes some excellent specimens from Corral Hollow, but I have been unable to find his locality. None of the localities in this region from which I have collected yield specimens as good or as abundant as the other localities noted in this paper.

From the discussions of these localities it is apparent that the San Pablo, and particularly the Neroly formation, changes from marine to continental as one progresses east and south. At the type section on the shores of San

Francisco Bay near Rodeo, the Neroly is almost wholly marine, as indicated by an abundant marine fauna, the absence of extensive crossbedding, the relatively good sorting of material, and the absence of leaves. One small layer of lignite about four inches thick is the only indication of terrestrial deposition that I have observed in this section. At Bailey Road and Loma Ranch marine and continental deposits are intermingled, and the formation as a whole suggests shoreline deposition. At Corral Hollow the Neroly appears to be wholly continental, as well as considerably thinner than elsewhere.¹ It may be significant also that the majority of land vertebrate remains have been recovered from the Neroly in this region and even farther south. This indicates that the sea in San Pablo time lay to the west, with land to the east. Whether this land was continuous to the foot of the Sierra is not known. Louderback² has suggested that the Neroly andesitic material was derived from the Sierran andesites. It has been considered that a sea occupied the Great Valley at this time. If this were so, it is difficult to understand how abundant andesitic material, especially the conglomerates, could be transported across it and come to rest on the opposite shore. But the presence of a sea in the Great Valley in Neroly time is not proved. Aside from the increasing continentality of the Neroly eastward, there is no exposure of marine sediments on the east side of the valley of the same age as Neroly or the andesitic river gravels of the Sierra.

There is another extensive occurrence of andesites that may have been from the same source as the Neroly material. North of San Francisco Bay, a series termed the Tolay volcanics³ underlie and intergrade with Petaluma sands and shales. Unconformably above the Petaluma are the Sonoma volcanics, which appear to interfinger with the marine Merced formation.⁴ This marine Merced has been dated by its invertebrate fauna as not older than Middle Pliocene. Horse teeth from the Petaluma beds have been determined by Stock⁵ to be a *Neohipparion* close to *N. gidleyi* which occurs in the Orinda. Thus the Tolay volcanics, with andesite in the upper portion, appear to occupy the same stratigraphic position as the Neroly. There are, however, several facts which are not in accord with this conclusion. First, basalt is interbedded with andesite in the upper portion of the Tolay and no basalt fragments have been reported from the Neroly. Second, Stirton believes the *Neohipparion* in the Petaluma beds to be of a type no older than upper Middle Pliocene.⁶ Third, the volcanics assigned to the Sonoma that interfinger with the Merced are not continuous with the Sonoma that over-

¹Huey, A., Stratigraphy of the Tesla Quadrangle, California. Paper read before the Geological Society of America, April 10, 1937.

²Louderback, G. D., Univ. Calif. Pub. Geol., vol. 15, No. 1, pp. 1-44, 1924.

³Morse, R. R., and Bailey, T. L., Geological Observations in the Petaluma District, Bull. Geol. Soc. Amer., vol. 46, pp. 1437-1456, 1935.

⁴Johnson, F. A., Geology of the Merced, Pliocene, Formation North of San Francisco Bay, California, unpublished, Univ. Calif. Library, 1934.

⁵Morse, R. R., and Bailey, T. L., *op. cit.*

⁶Stirton, R. A., Age of the Tertiary Mammalian Remains from the San Francisco Bay Area, Univ. Calif. Pub. Geol. *In press.*

lies the Petaluma, and fourth, 20 miles east of the town of Petaluma, in Solano County, light blue-gray sands with a fauna having San Pablo affinities lie unconformably below interbedded andesitic and basaltic flows, tuffs, breccias, and pebble conglomerate and sandstone that are lithological duplicates of the upper part of the Tolay volcanics at Petaluma. These considerations tend to make the Tolay volcanics very questionably related to the Neroly andesitic material. As far as present knowledge goes, the weight of evidence is far heavier for a Sierran source for the Neroly material than for a Coast Range source.

The Neroly formation, then, appears to have been deposited partly in a sea that extended westward, and partly on land farther east, by streams flowing westward from the Sierra, during a time when abundant andesitic material was being added to them. The gradients of these streams were low, but they were not yet at grade, as is indicated by the occasional conglomerates they deposited. Along the shores of the sea were lagoons and bars, somewhat similar to the present conditions along the east coast of the United States. As the sediments were being deposited in this area, sinking of the substratum occurred, so that the upper part of the Neroly was deposited at about the same level in relation to the sea as the lower part.

COMPOSITION OF THE FLORA

Twenty-six species representing 25 genera have been collected from the San Pablo beds. They are distributed among 21 families and 17 orders. Among them are a pteridophyte, 2 gymnosperms, and 3 monocotyledons. All of the remainder are dicotyledons, of which 1 is gamopetalous and 19 are choripetalous. Three species are herbaceous, 3 are shrubs, 3 are vines, and 17 are arborescent. The systematic list follows:

PTERIDOPHYTA

EQUISETALES

Equisetaceæ

Equisetum sp.

SPERMATOPHYTA

GYMNOSPERMÆ

CONIFERALES

Taxodiaceæ

Taxodium dubium Heer

Taxaceæ

Taxites olriki (?) Heer

ANGIOSPERMÆ

MONOCOTYLEDONÆ

PANDANALES

Typhaceæ

Typha sp.

GRAMINALES

Gramineæ

Poacites sp.

LILIALES

Liliaceæ

Smilax diforma n. sp.

DICOTYLEDONÆ

SALICALES

Salicaceæ

Salix sp.

Populus balsamoides

Goeppert

Populus emersoni n. sp.

MYRICALES

Myricaceæ

Myrica diforme (Sternberg) Chaney

JUGLANDALES

Juglandaceæ

Juglans oregoniana Lesquereux

FAGALES

Betulaceæ

Alnus corrallina Lesquer-
eux*Betula multinervis* Jen-
nings

Fagaceæ

Castanea castaneæfolia
Knowlton

RANALES

Magnoliaceæ

Magnolia californica Les-
quereux

Lauraceæ

Persea princeps Schimper
Umbellularia oregonensis

Chaney

ROSALES

Platanaceæ

Platanus dissecta Les-
quereux

Rosaceæ

Prunus chaneyi n. sp.*Rosa hillæ* Lesquereux

SAPINDALES

Aquifoliaceæ

Ilex lomensis n. sp.

RHAMNALES

Rhamnaceæ

Berchemia multinervis

Heer

PARIETALES

Dilleniaceæ

Tetracera castaneæfolia

MacGinitie

UMBELLALES

Cornaceæ

Nyssa knowltoni Berry

MYRTALES

Myrtaceæ

Myrtus oregonensis Les-
quereux

OLEALES

Oleaceæ

*Chionanthus membran-
aceus* Knowlton

INCERTÆ SEDIS

Fruit (?)

The flora is preserved chiefly as leaf impressions, with only *Taxodium* and *Nyssa* represented by fruiting structures. Twigs, roots, and bark, largely unidentified, have been found also.

A precise quantitative analysis of the flora is not considered worthy of inclusion in this paper, yet the approximate presentation of such a study may serve to bring out certain important conclusions regarding the nature and the distribution of the San Pablo vegetation. These data have been summarized in table 1.

Reference to this table reveals some critical facts. *Taxodium dubium*, a tree which sheds its leaves abundantly and lives in the sites of deposition, is represented by the largest number of specimens. *Nyssa*, a tree of similar habits, is also abundant. It should be stated that the figure representing the abundance of this tree was obtained by counting both the seeds and the leaves, and the seeds were much more abundant than the leaves. Since the leaves of *Nyssa* are thin and large and consequently not well suited for preservation, the fact that any of them at all were preserved is an indication that the trees were close to the sites of deposition. The seeds, of course, are much more durable, and might be preserved both close to and far removed from the trees which were their source. The abundance of *Juglans* is not wholly consonant with the implied habits of this tree. However, numerical count is based on the number of leaflets in the flora, not on the number of leaves. Since there are up to twenty leaflets per leaf in *Juglans*, the actual proportion was less than is indicated in the leaf count.

The abundance of birch, alder, willow, and the poplars may be explained by the nature of the leaves of these trees in conjunction with their habitats. All of them are stream border types, and all of them have fairly small hard leaves that can be transported long distances without suffering destruction. In almost every case these leaves are more abundant at Localities 618 and 199 than they are at Locality 607. As I have shown in the discussion of the lithology of the San Pablo, the sediments in which the leaves occur, suggest that they were deposited in quiet pools such as might occur in swampy regions or the sloughs and backwaters of deltas. At Localities

TABLE 1—Relative abundance of San Pablo species

Species *	Locality				Approximate percentage of total
	607	618	199	P361	
<i>Taxodium dubium</i>	A	R	12.0
<i>Alnus corrallina</i>	R	C	A	...	12.0
<i>Betula multinervis</i>	R	C	A	...	11.0
<i>Nyssa knowltoni</i>	A	...	R	...	9.0
<i>Juglans oregoniana</i>	A	...	A	...	9.0
<i>Populus balsamoides</i>	C	A	R	C	9.0
<i>Populus emersoni</i>	C	A	C	C	7.0
<i>Poacites sp.</i>	A	A	R	C	7.0
<i>Persea princeps</i>	A	C	C	A	7.0
<i>Salix sp.</i>	C	A	C	...	4.0
<i>Platanus dissecta</i>	C	C	R	R	3.0
<i>Equisetum sp.</i>	R	C	R	...	3.0
<i>Prunus chaneyi</i>	C	R	C	R	2.0
<i>Typha sp.</i>	C	R	1.0
<i>Rosa hillii</i>	R	R	1.0
<i>Berchemia multinervis</i>	R	1.0
<i>Ilex lomensis</i>	R	0.6
<i>Magnolia californica</i>	R	R	...	R	0.5
<i>Smilax diforma</i>	R	0.4
<i>Umbellularia oregonensis</i>	R	0.4
<i>Chionanthus membranaceus</i> ...	R	...	R	...	0.3
<i>Myrica diforme</i>	R	0.3
<i>Castanea castanæfolia</i>	R	0.2
<i>Tetracera castanæfolia</i>	R	0.1
<i>Taxites olriki</i> (?).....	R	0.1
<i>Myrtus oregonensis</i>	R	0.1

* The species are arranged in order of their abundance in the collections. "A" indicates abundant; "C" indicates common; and "R" indicates rare in proportion to the collections at each locality.

618 and 199, on the contrary, the sediments suggest a closer association with running water, such as might occur at the actual mouths of contributory streams. If this is actually the case, it is to be expected that leaves of stream border species would be more abundant in such situations than in regions farther removed from the stream mouths.

The relative abundance of *Persea* may be explained by the durability of its leaves, which would enable them to withstand the vicissitudes of transportation and burial. It is to be noted that these leaves are com-

mon at all localities, a response to the habitat of the tree and to the strength of its leaves. The abundance of grass and *Equisetum* is no doubt due to their habit of growing close to quiet pools and along the banks of flowing streams. The rarity of *Typha* is hard to explain; it may be due to the fact that cat-tail stems float longer and are consequently carried farther away before sinking. This explanation does not wholly satisfy me, yet it is difficult to account for the rarity of this species as due to the accidents of collection. The rarity of *Magnolia* is also difficult to explain. The leaves of this tree are thick and substantial, and it probably grew near the borders of the pools and swamps of the region. Under these conditions, there should have been more leaves entering the record. Nevertheless, recognizable remains of this tree are rarely encountered in the San Pablo beds. The remaining species are all rare; all of them probably lived a considerable distance from the sites of deposition, and, unlike birches and alders, did not possess leaves of sufficient durability to become commonly preserved.

One of the interesting points brought out during the study of this flora is the complete absence of oak leaves. Several oaks are abundant today in situations occupied by the living equivalents of the San Pablo flora; many fossil species have been recorded in deposits of Cretaceous age and younger throughout the northern hemisphere. Leaves of oaks are easily recognized, and of such a nature that they should be preserved. Nevertheless, of almost a thousand specimens collected from the San Pablo localities, all those which resemble oaks are found upon careful comparison with modern plants to resemble more closely some other genus. It is difficult to believe that chance is responsible for the failure to find any remains of oaks in this flora. Consideration of fossil floras suggests an explanation for their absence. In temperate and warm temperate floras of pre-Pliocene age, oaks are common only in those regions that were not adjacent to the sea, such as the Mascall, Latah, and Bridge Creek. In the case of floras closer to the coast, oaks are much rarer. In the Weaverville flora, for example, MacGinitie¹ records only one species of oak in a flora of 37 species; this species is represented by 20 specimens out of more than 2700. Oaks are equally rare in the older floras of a more tropical aspect from northern California and Oregon. These facts, together with the absence of oaks in the San Pablo flora, may indicate that oaks did not occupy lowlands adjacent to the sea in northern regions before Pliocene times. Berry² records 4 species of oaks in a flora of 18 species from the Pliocene Citronelle formation, indicating that on the east coast of this continent, at least, oaks had reached their present position at that time. The evidence for the west coast is less exact. Dorf³ discusses floras from 7 formations of Pliocene age in California. Two

¹ MacGinitie, H. D., Carnegie Inst. Wash. Pub. No. 465, III, 1937.

² Berry, E. W., U. S. Geol. Surv. Prof. Paper 98-L, 1916.

³ Dorf, E., Carnegie Inst. Wash. Pub. No. 412, 1933.

of these are fresh-water, with oaks common. Three are marine, with oaks absent, except at one locality in one formation, which at this place is doubtfully marine. Two are shoreline deposits, with conditions of deposition similar to those of the Neroly. In these two, oaks are common. This indicates that oaks had invaded lowlands by Pliocene times on the west coast as well as the east coast. The absence of oaks from the San Pablo flora is a striking example of the profound changes in tolerance that may occur in a genus over a relatively short period of time. I think it may be safely concluded that oaks were not present in the San Pablo flora, because the chances of leaves being present but not preserved or found are too remote for reasonable consideration.

ECOLOGICAL CONSIDERATIONS

The San Pablo contains relatively few species, but fortunately a large proportion of them are of distinct ecological significance, and thus definitely suggest conclusions concerning the conditions under which they grew. Table 2 shows the related modern species of the fossil species as they are at present determined.

TABLE 2—San Pablo species and their living equivalents

San Pablo species	Living equivalent
Equisetum sp.	E. arvense Linné ?
Taxites olriki (?)	{ T. brevifolia Nuttall
	{ T. floridana Chapman
Taxodium dubium	T. distichum Richard
Typha sp.	Typha sp.
Poacites sp.	Not known
Smilax diforma	S. rotundifolia Linné
Salix sp.	{ S. nigra Marsh
	{ S. longipes Anderson
Populus balsamoides	P. grandidentata Michaux
Populus emersoni	P. trichocarpa Torrey & Gray
Myrica diforme	M. asplenifolia Linné
Juglans oregoniana	J. nigra Linné
Castanea castanæfolia	C. pumila Miller
Alnus corrallina	A. rhombifolia Nuttall
Betula multinervis	B. lenta Linné
Magnolia californica	M. grandiflora Linné
Persea princeps	P. borbonia Sprengel
Umbellularia oregonensis	U. californica Nuttall
Platanus dissecta	P. occidentalis Linné
Prunus chaneyi	P. serotina Ehrhart
Rosa hilliæ	{ R. nutkana Presl.
	{ R. woodsii Lindley
Ilex lomensis	I. opaca Aiton
Berchemia multinervis	B. scandens Trelease
Tetracera castanæfolia	T. volubilis Linné
Myrtus oregonensis	M. communis Linné
Nyssa knowltoni	N. aquatica Linné
Chionanthus membranaceus	C. virginicus Linné

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The flora may be divided into several elements, not with the implication that the species were rigidly distributed only among the habitats to which they are assigned, but merely as a means, more or less artificial, of clarifying the reconstruction of the fossil flora in terms of equivalent living vegetation. These are termed the *Taxodium-Nyssa* Element, the Swamp-border Element, the Stream-border Element, and the Dry-soil Element.

No element herein discussed possesses all the species present in the modern forest to which it is related. Accidents of preservation and collection are sufficient to preclude such a condition; in addition is the far more important factor of detailed changes in the composition of the elements in the time interval since the Upper Miocene. The distribution of a species depends primarily upon its tolerance opposed by habitat conditions throughout the world. As pointed out by Good,¹ there is no reason to believe that the tolerance of any particular phylad of plants has not changed during the time since its first appearance. Tolerance is a specific character, and like any other specific character is subject to evolution. Thus, except in the case of the most recent fossil floras, one would not expect to find a fossil association exactly duplicated by a living one. Nevertheless, while individual species may have had their tolerances altered during geological time, there is little likelihood that every member of an association will have changed in exactly the same way, so that the implications of a fossil association, when compared with a living one, may be regarded as reasonably accurate.

The primary element of the San Pablo flora, termed the *Taxodium-Nyssa* Element, is the most definitive one. The following species are considered to have belonged to it:

Taxodium dubium
Nyssa knowltoni
Typha sp.
Equisetum sp.
(*Poacites* sp. ?)

The living equivalents of the two trees in this association are the bald cypress and the tupelo. These trees are typically developed in the deep swamps of the southeastern coastal plains. Their range is extended northward to Delaware and westward to Texas. A close relative of the bald cypress is found in Mexico, where *Nyssa* does not appear. They are associated with a small number of other species, with the sweetgum, water locust, planer tree, and certain ashes prominent. No leaves referable to these associates have been found in the San Pablo beds, although some of them are to be expected. The presence of the two trees *Taxodium* and *Nyssa*, an association which is very narrowly restricted to a particular habitat today, strongly suggests the conditions under which the San Pablo

¹ Good, R. D., *New Phytologist*, vol. 30, pp. 149-171, 1931.

flora was deposited, even though other species which might be expected have not been found.

Associated with this arborescent group was a herbaceous group consisting of the remaining genera listed above. The first two are undoubted swamp types. Both the cat-tail and the scouring rush are common in swamps and extremely moist places throughout the world. Specific identification of the San Pablo material is impossible, so no closer reference is justified. The grass (*Poacites*) may have been a swamp type, or it may have been an occupant of the uplands. No indication of the genus is available in the material preserved, but the abundance of the remains suggests that it was a type which grew close to the sites of deposition, that is, in the swamps or in grassy glades adjoining them. On the other hand, the nature of the sediments in which the leaf impressions are found indicates that the grass blades may have been transported for somewhat greater distances. The fragmentary nature of the remains lends support to this alternative.

A second element represented in the San Pablo flora is the Swamp-border Element. It contains the following species:

Persea princeps
Magnolia californica
Berchemia multinervis
Smilax diforma

All of these species are similar to species growing today in the southeastern states along the borders of swamps and in places of less than maximum ground moisture. Some of them less commonly grow in the drier places such as the pine barrens and sand hills of the region. They are best developed when occurring in the more moist places in association with *Quercus laurifolia* Michx., *Q. nigra* L., and *Prunus caroliniana* Ait. The small representation of this element in the fossil collections may be explained the same way as in the case of the *Taxodium-Nyssa* Element. It is due to incomplete representation in the collections, and to tolerance changes among certain species that are now associated with the elements. Furthermore, perhaps some of the species placed in the next element may with equal propriety be assigned to this element.

A third element in the San Pablo flora is called the Stream-border Element, to distinguish it from the Swamp-border Element. The following species represent this element:

Salix sp.
Populus balsamoides
Juglans oregoniana
Alnus corallina
Platanus dissecta
Betula multinervis
Prunus chaneyi
Ilex lomensis
Chionanthus membranaceus

This is by far the largest single group in the flora. All of its members have close living relatives whose ranges include the southeastern states, although some of them extend into regions with far different climates from that which occurs in those states. This group in general is distributed along stream borders on the edge of the *Taxodium* forest, under similar climatic conditions but with a consistently drier substratum. Its members are ideally situated to have their leaves enter the record, even though they may be removed some distance from the basins of deposition, since they border streams that drain into the basins. They were presumably more favorably situated in this respect than the Swamp-border Element, since the latter lived where most of their leaves would drop in quiet waters of the actual swamp and rot, instead of in places where rapid sedimentation was occurring. This may be a factor in the greater representation of the former element in the fossil collections. The majority of the species of this association preserved have fairly tough leaves, able to withstand transportation without destruction. As in the case of the other groups or elements discussed, many members of the comparable modern group are not represented in the fossil group.

A fourth group may be mentioned, called the Dry-soil Element. This group contains:

Populus emersoni
Myrica diforme
Castanea castaneæfolia
Umbellularia oregonensis
Rosa hilliæ

This group is rather heterogeneous, and in some respects the most interesting. Only one of its members, *P. emersoni*, is abundantly preserved. It represents a tree now living in western United States, and is closely related to fossil species that in Miocene times inhabited regions farther north than the San Pablo flora. It evidently was a species closely related to *Populus eotremuloides*, but with its tolerance altered to permit it to occupy warmer regions. Perhaps *Populus deltoides* Marsh is a descendant of the San Pablo species, since the leaves of the two species are similar, and the fruiting structures of *P. trichocarpa* and *P. deltoides* are not greatly different. If such is the case, *P. emersoni* has a living equivalent in the southeastern states. Another member of the Dry-soil Element, *Umbellularia oregonensis*, has a living equivalent in the far western states. *Rosa hilliæ* has been compared to a western species, although it resembles as closely a species whose range is farther east. *Myrica diforme* has a living equivalent in the northeastern states and Canada, but its southern limits closely approach the northern limits of the bulk of the modern equivalents of the San Pablo species. Only one species, *Castanea castaneæfolia*, is represented by a modern equivalent which grows in the same region as the bulk of the

flora. Except for *Populus*, the species of this element are sparsely represented. Evidently they occupied areas that afforded them little chance of entering the record, and possibly they were rare in the region at the time the beds were deposited. All of them are common in Miocene floras farther north, and some are abundant. It would appear that the southern limit of these species was near the area in which the San Pablo beds were laid down, and they extended into the area at that time only in its drier portions.

As brought out in the foregoing discussion, the majority of the living equivalents of the San Pablo species occupy the southeastern coastal plain. The typical *Taxodium* forest ranges around the Atlantic and Gulf of Mexico coasts from Delaware to eastern Texas, and up the Mississippi Valley almost to the Ohio River. The fossil flora as a whole suggests conditions more like those that prevail on the border of this forest, rather than those that occur in the places where it reaches its best development. The absence of the *Taxodium-Nyssa* associates, such as *Quercus nigra* and *Fraxinus caroliniana* Mill., and the prominence of the relatively dry substratum, the northern and the western types such as those included in the Stream-border and Dry-soil Elements indicate that climatic conditions approached those of the northern borders of the bald cypress forest rather than those of the typical swamp regions. Too much weight must not be given to the evidence of the presence of *Taxodium* and *Nyssa*, since these two genera may have had their tolerance altered to permit them to occupy swamplier and more southern places than they did formerly. Both have species that still live in more normal conditions than those offered by the acid swamps that are the present habitat of the species to which the fossils are referred. The evidence of the fossil record of these trees indicates that they have been progressively crowded southward during the Tertiary. This crowding, augmented perhaps by Pleistocene glaciation, may have resulted in forcing these trees to become adapted to the relatively unfavorable conditions of the swamps which occupied most of the southern lowland region available to them. It is probable that the present restriction of *Taxodium distichum* and *Nyssa aquatica* to swamps was not also true for their Tertiary ancestors. In any case, it seems clear that if the San Pablo flora as a whole had lived in a swamp, there would be a greater proportion of ancestors of present swamp types included in the collections. Likewise, the presence in the flora of a large group of plants now limited to areas adjacent to swamps indicates that conditions of deposition were not typical of true swamps. The absence of swamp-like sediments in the San Pablo formations supports this conclusion. But this statement does not mean that drainage or climatic conditions were greatly different from those of the present *Taxodium* forest. If they had been one would expect to find a flora comparable to those now existing either to the north or to the west of the range of this forest. These two conditions are exemplified by the Mascall flora, studied by Chaney and

others, and by the High Plains flora, recently discussed by Chaney and Elias.¹ The latter flora is altered from the assemblage expected because of its younger age, yet it partially represents the type of vegetation that would occur if conditions had been similar to those prevailing on the present western border of the *Taxodium-Nyssa* forest. The Mascall, and even more the Bridge Creek floras, have, in addition to a large western element, a group of fossils representing the present forests of the eastern states north of the *Taxodium* forest.

A map was made in connection with these studies on which the range of each living equivalent of the San Pablo species was shaded lightly. This map when completed showed the deepest color, and hence the greatest concentration of indigenous species, in the region in which trees of southern distribution, such as *Taxodium distichum*, *Nyssa aquatica*, *Persea borbonia*, and *Magnolia grandiflora*, and those of northern distribution such as *Myrica asplenifolia*, *Populus grandidentata*, and *Betula lenta* all occur. Evaluating the diverse ranges of the species related to the San Pablo species and presumably requiring approximately the same conditions, it is considered that the flora was deposited under conditions similar to those that now prevail near the northern border of the *Taxodium-Nyssa* forest in the region just south of Chesapeake Bay.

CLIMATIC IMPLICATIONS

As long ago as 1910 J. P. Smith² stated that the flora of the San Pablo indicated that the climate of the time was slightly warmer than the present one, with rainfall either more abundant or more evenly distributed throughout the year. In 1915 Clark,³ on the basis of the geographical range of the Recent species in its invertebrate fauna, stated that the waters of the San Pablo sea were of about the same temperature as the waters of the Pacific Ocean between Point Conception and Santa Barbara, California. The present mean annual temperature of that region is about 60° Fahrenheit.

Table 3 presents data for the regions which today support a flora most similar to the San Pablo flora. The first column is probably the most accurate, not only because tidewater Virginia is the place where the greatest number of living equivalents of San Pablo species occur, but also because it lists the conditions in the particular ecologic situation in which the flora was deposited. The figures for the other two coastal states represent means for the coastal areas and the more mountainous parts together, and consequently do not as accurately indicate the conditions along the coast. Missouri has been included because it is also a region of the northern limit of the *Taxodium* forest, but Missouri has a continental climate, which the San Pablo flora certainly did not. Furthermore, the

¹ Chaney, R. W. and Elias, M. K., Carnegie Inst. Wash. Pub. No. 476, I, 1936.

² Smith, J. P., Popular Science Monthly, May 1910.

³ Clark, B. L., Univ. Calif. Pub. Geol., vol. 8, No. 22, pp. 385-572, 1915.

Taxodium forest does not extend very far north in the state, and the figures are averages for the whole state, and so are different from the conditions that occur in regions of the *Taxodium* forest. For instance, the mean annual temperature for the state as a whole for 1931 was 58.0°, and for Caruthersville, in the southern part of the state, the region in which *Taxodium* grows, was 63.3°. This illustrates the difference between figures for the state as a whole and for the portion of it that concerns us here.

TABLE 3—Climatological data for *Taxodium* forest border areas

Month	Tidewater Virginia		North Carolina		Maryland		Missouri	
	Temp.	Precip.	Temp.	Precip.	Temp.	Precip.	Temp.	Precip.
January.....	40.0	3.03	41.2	3.87	32.9	3.22	30.5	2.04
February.....	40.1	3.60	42.6	4.12	34.0	3.08	32.4	2.11
March.....	47.5	3.83	49.9	4.20	43.0	3.43	43.9	3.02
April.....	56.2	3.37	57.9	3.52	52.4	3.57	55.1	3.81
May.....	65.1	3.51	66.8	4.18	62.4	3.37	64.4	4.67
June.....	73.3	4.14	73.8	4.79	70.8	3.93	73.2	4.87
July.....	77.5	4.85	76.9	5.84	75.2	4.21	77.3	4.00
August.....	76.2	5.06	75.8	5.56	73.2	4.31	76.0	3.75
September.....	71.0	3.68	70.9	3.98	67.8	3.22	69.0	3.84
October.....	60.3	2.98	59.9	3.34	56.4	2.88	57.4	2.89
November.....	49.9	2.28	49.9	2.53	45.1	2.55	44.4	2.40
December.....	41.1	3.65	42.5	3.85	35.4	3.16	33.9	2.07
Means.....	58.2	...	59.0	...	54.8	...	55.8	...
Totals.....	...	43.98	...	50.78	...	40.93	...	39.47

Temperatures are in degrees Fahrenheit.

Precipitation is in inches.

These data are extracted from U. S. Department of Agriculture, Weather Bureau, Climatological Data for the United States by Sections, vol. 18, 1931.

The table shows that the mean annual temperature for the tidewater region is about 58°, increasing southward and decreasing northward. The coldest month is January, with a mean of 40°, indicating that frosts are neither common nor severe. The six months from May to October have mean temperatures above 60°, indicating a long warm summer. The annual precipitation is about 44 inches, which likewise increases southward and decreases northward. The distribution of the precipitation over the year is uniform; the driest month (November) has over two inches. The six warmest months have abundant moisture, especially the first five. This results in a long growing season. In Missouri the mean annual temperatures are lower, reflecting the lower winter temperatures. Rainfall in Missouri is somewhat lower, with the peak occurring in June instead of in August, as it does in Virginia. The values for the warmest and coldest

months in Missouri are several degrees farther removed from the value for the yearly mean than is the case in Virginia. As stated above, it must be remembered that these figures, representing an average for the state, are more extreme than they should be to depict accurately the climate in the part of Missouri that supports the *Taxodium* forest.

After having investigated the climatic indications of the larger part of the flora (in the section on ecological considerations), it is pertinent to inquire into the possibility of the remaining species existing under such conditions. *Populus trichocarpa* is common at higher elevations and latitudes than is to be expected for a member of this flora; however, it lives as low as 500 feet in the Santa Barbara National Forest in southern California, where temperature conditions are about the same as in tide-water Virginia. Throughout its range, either it is limited to regions of abundant rainfall, or in places with a long dry season it occurs only along streams or where there is a large amount of ground water. *Umbellularia californica* also occurs well to the south. It is present in Riverside County, California, in canyons on the west side of the San Jacinto Mountains. These canyons have a constant and abundant supply of ground water. *Tetracera volubilis* is a vine commonly found in low latitudes in forests that are somewhat drier than a typical tropical rain forest. Its climatic requirements are considerably different from the rest of the modern related species of the San Pablo flora. However, it is possible that the mild winters postulated for the San Pablo time permitted the growth of a few individuals in particularly favored spots in which the conditions approached those of the drier portions of a rain forest. Middle Tertiary members of this genus have been recorded elsewhere in western America in association with plants which are considered to indicate temperate or warm temperate climates. *Rosa woodsii* occurs in Missouri, which has climatic conditions not greatly different from the *Taxodium* forest. *Rosa nutkana* seems to be limited to regions that are slightly colder than the *Taxodium* forest, although it requires similar moisture conditions. Thus we see that the climatic conditions determined for the San Pablo flora on the basis of the greater part of the flora are equally suitable for the lesser part; the reasons for the present geographic separation of the two parts may be revealed by a more complete knowledge of plants and their histories. *Alnus rhombifolia* is another western species which, while not growing with the majority of the descendants of the San Pablo flora, requires approximately the same conditions. It is distributed through the Coast Ranges along streams and where the soil is constantly wet, a condition that has the same effect as abundant summer rain. Its temperature requirements are approximately the same as some of the more northerly distributed eastern descendants of the San Pablo species.

There is indicated only a slight change in temperature conditions between San Pablo and Recent times; it may have been a few degrees warmer

in the past. Rainfall conditions, however, show a profound change. Not only is the rainfall much less at present, but it is limited almost completely to the late winter and spring months. It is possible that the fossil flora was able to survive without summer rain, perhaps with abundant summer fog, but the evidence strongly indicates that rain did occur. The nature of the sediments, as discussed above, supports this. At every point where leaves occur, the sediments indicate fluvial deposition. These are spread over a large area. In order to furnish enough water for so many streams, or for such a large stream, rainfall must have been more abundant than at present in the same region. Floras of similar age in western America, reported upon by LaMotte¹ and MacGinitie,² all indicate that rainfall was abundant in summer as well as winter. It should be noted that at Altamont Pass (Locality 199) many leaves are found very closely curled. This is usually taken to mean subaerial deposition, since leaves that are buried in water are usually softened and lying in planes parallel to the bedding planes. This may mean that the streams of the region were seasonal, or it may indicate that deltas with dunes and sandspits or other temporarily dry areas were present. The almost total absence of these curled leaves at the other localities favors the latter alternative. Such sandy dry spots are closely associated with the *Taxodium-Nyssa* forest, especially along its borders, and it is not strange to find evidence of similar areas in association with the San Pablo flora.

AGE OF THE FLORA

The age of the upper member of the San Pablo Group has been a matter of disagreement among geologists and paleontologists for many years. In 1915 Clark³ gave a summary of the opinions published up to that time. In this paper he stated his opinion, based on the percentage of Recent species in the invertebrate fauna of the Neroly, that the age of the formation was Upper Miocene. He suggested the possibility of Lower Pliocene age but favored the earlier age. In 1924 Louderback⁴ included a short discussion of the published opinions concerning the age of the San Pablo, but gave no new evidence.

Recent work by Stirton on the mammalian remains found in the Upper San Pablo leads him to believe that these beds are Lower Pliocene. He has determined mammalian remains found with Upper San Pablo invertebrates as typical Lower Pliocene forms, on the basis of their evolutionary development.⁵

¹ LaMotte, R. S., Carnegie Inst. Wash. Pub. No. 455, V, 1936.

² MacGinitie, H. D., Carnegie Inst. Wash. Pub. No. 416, II, 1933.

³ Clark, B. L., Univ. Calif. Pub. Geol., vol. 8, No. 22, pp. 385-572, 1915.

⁴ Louderback, G. D., Period of Scarp Production in the Great Basin, Univ. Calif. Pub. Geol., vol. 15, No. 1, pp. 1-44, 1924.

⁵ Stirton, R. A., Age of Tertiary Mammalian Remains from the San Francisco Bay Area, Univ. Calif. Pub. Geol. *In press*.

The opinions of Clark and Stirton represent the two viewpoints concerning the age of the Neroly. All workers agree that it is close to the Miocene-Pliocene boundary, and the question naturally arises whether, in the case of evidence based on two different groups of organisms, a simultaneous boundary for both can be agreed upon. If, as may be the case, the Neroly represents a transitional deposit between the Miocene and the Pliocene, the appearance in it of a new form used to mark a new period is controlled by migration as well as time. Similarly, a certain group of organisms, especially if they are marine and subject to less rapidly changing conditions than land forms, could conceivably exist a short time beyond the period of which they are characteristic. It may be pointed out that the vertebrate evidence is weakened by the following considerations: the fauna now known is meager, consisting of a few horse teeth only; and the Miocene faunas of central California are practically unknown. This makes it necessary to compare the San Pablo forms with a fauna from the Great Plains, which, while furnishing an excellent succession, lived in a very different habitat from the region under discussion. The additional evidence offered by fossil plants to this discussion is set forth below.

TABLE 4—Distribution of San Pablo species in other fossil floras

Species	California Pliocene	Citronelle	Weiser	Mascall *	Latah	Bridge Creek	Missoula	Weaverville	Eocene—all western America
<i>Taxodium dubium</i>	X	X	X	
<i>Taxites olriki</i> (?)	X	X
<i>Myrica diforme</i>	X	
<i>Juglans oregoniana</i>	X	X	
<i>Alnus corrallina</i>	X	X	
<i>Betula multinervis</i>	X	
<i>Castanea castanæfolia</i>	X	
<i>Magnolia californica</i>	X	X
<i>Persea princeps</i>	X	X	
<i>Umbellularia oregonensis</i>	X	X	X	
<i>Platanus dissecta</i>	X	X	X	X	
<i>Rosa hilliæ</i>	X	X	
<i>Berchemia multinervis</i>	X	X
<i>Tetracera castanæfolia</i>	X	
<i>Nyssa knowltoni</i>	X†	X	X	
<i>Chionanthus membranaceus</i>	X
Total species 16.....	1	2	1	4	7	4	2	6	4

* Including the Trout Creek, Blue Mountain, and Cedarville.

† Perhaps not the same species; but every indication suggests that *N. aquaticaformis* is the same as *N. knowltoni*.

Table 4 shows the distribution of San Pablo species in certain other Tertiary floras of western America, and in a Pliocene flora of the east coast (the Citronelle). Only those forms from the San Pablo that have been identified specifically are included in this table; the others will be mentioned where it is considered that they may bear some significance. Only one species, *Umbellularia oregonensis*, has been noted from the Pliocene floras of California. This is almost identical with *U. californica*, still present in California. It is rare in the San Pablo collections, and as discussed above, is considered to have been uncommon in the San Pablo forests. In addition, three genera are represented in the San Pablo and the California Pliocene floras by species that suggest close relationships. *Ilex lomensis* and *Populus emersoni* are discussed in the systematic portion of this paper, and the Pliocene *Platanus paucidentata* has long been considered a descendant of *Platanus dissecta*, having evolved under the influence of increasing aridity. All four of these genera belong either to the Stream-border or to the Dry-soil Element in the San Pablo flora. This is to be expected, since the Pliocene floras consistently indicate drier conditions than the San Pablo flora, and only the San Pablo species with a tendency toward tolerance for dry conditions would persist into a time when aridity was more pronounced.

One species (*Platanus dissecta*) occurs in the Weiser flora, with three genera which might show relationships if they could be accurately identified. These are the *Equisetum*, the *Typha*, and the grass. This does not indicate any close similarity of the two floras. Dorf¹ believes the Weiser to be Upper Miocene or Lower Pliocene, favoring the later age. Having in mind the difference in latitude as well as the relative position in regard to the sea and mountains of the two floras, it is clear that they were not in the same climatic province. Even though they are of approximately the same age, they would have but few species in common. The one species present in both has a living equivalent which ranges through a greater interval of latitude than that between the two floras.

While only two species occur in the Citronelle flora, they are among the most abundant in the San Pablo, and make up 20 per cent of the total flora, and over a third of the species with outside distribution. This offers little evidence of contemporary age for the floras, since the history of the two sides of North America has been quite different. Largely unaffected by the general desiccation that has been noticed on the west coast, the east coast has retained conditions suitable for the development of the *Taxodium-Nyssa* forest up to the present day.

The San Pablo shows greater similarity to the Latah than to any other flora. The Latah was far inland at the time of its deposition, and was probably east of at least low mountains, as well as considerably farther north. In addition to the seven species listed in table 4,

¹ Dorf, E., Carnegie Inst. Wash. Pub. No. 476, II, pp. 98-104, 1936.

4 forms not specifically identified may also be common to both. Berry¹ regards the Latah as Upper Miocene; an increasing body of evidence indicates it to be more nearly Middle Miocene. The composition of the Latah flora compared with the Mascall appears to represent somewhat warmer conditions. In the light of what is known of Tertiary paleobotany in western America this would indicate that the Latah is slightly older than the Mascall. If the Latah was in fact growing under warmer conditions, it is difficult to account for a flora indicating a colder climate farther south at a later time. As will be brought out below, the compositions of these two floras can be explained on the basis of precipitation distribution rather than temperature distribution during this time. In considering the Latah flora it is well to remember that it is composed of several distinct groups of plants that are not today closely associated. In addition to the element like the San Pablo flora, there is a more temperate or upland element, and a smaller more tropical element. The more temperate element of the Latah is represented in the Mascall flora: 21 species are common to both floras. Four San Pablo species occur in the Mascall, and 7 in the Latah. With one exception, these are all different species; that one (*Platanus dissecta*) is today represented by a species with a wide range. Berry states that the climate of the Latah flora was similar to that which now exists in Maryland and adjacent regions. I have shown above that the San Pablo probably lived under similar climatic conditions. The inland intermontane position of the Latah formation is probably the explanation for the heterogeneity of its flora, with the warmth-requiring species occupying the lowlands and the drier cooler species on the adjacent elevations. When considering the age of the Latah in relation to the Mascall and the San Pablo it is necessary to give most weight to the evidence offered by the species of the same topographic habitat. Thus the lowland element of the Latah is more significant than the upland since it corresponds to the habitat of the San Pablo. The more northerly position of the Latah indicates that it is older than the San Pablo. In the case of the Mascall, the element of it that was nearest to the basins of deposition is about the same as the element of the Latah that was considerably removed from them. Owing to the secular drying throughout the Tertiary, elements moved down the slopes, so that by Mascall time the upland element of the Latah had come to occupy a lowland position. This indicates that the Latah is older than the Mascall also. These considerations tend to show that the Latah and the San Pablo floras bear the same climatic relationships to the Mascall, but not that the three floras are the same age.

The relations of the Bridge Creek flora to the Mascall and the San Pablo also have some bearing on this problem. In the Bridge Creek flora of the Crooked River Basin,² in addition to the redwood element, there are a

¹ Berry, E. W., U. S. Geol. Surv. Prof. Paper 154-H, 1929.

² Chaney, R. W., Carnegie Inst. Wash. Pub. No. 346, IV, pp. 45-138, 1927.

number of forms with descendants now living in the eastern part of northern United States, such as *Carpinus grandis*, *Fagus pacifica*, *Ostrya oregoniana*, *Platanus aspera*, *Ulmus speciosa*, and others. This group suggests a climatic and latitudinal relation to the San Pablo flora similar to the one that exists between the living equivalents of the two groups today. By the time of the deposition of the Mascall flora, which occupied the same general area as the Bridge Creek, topographic changes to the west had reduced rainfall in what is now central Oregon, with a consequent reduction of the eastern summer rain types and of the more mesic western types such as *Sequoia*. The relationships of the Bridge Creek, the Latah, and the Mascall floras suggest that temperature changes that occurred in the time interval including the deposition of these three floras were not as prominent as the generalized statements¹ of the climatic development of the Tertiary are frequently taken to mean. Dorf² has recently brought out evidence to show that temperature changes, especially changes in mean annual temperatures, were very small from the time of the deposition of the first of these floras to the time of deposition of the last of them. It should be pointed out that the time interval involved is not now considered as great as was formerly thought to be the case, and that the living equivalents of the species particularly concerned all occupy regions in which there is very little temperature contrast between the warmest and the coldest. It may be concluded that the general cooling from the Bridge Creek age to the deposition of the Weiser beds was not pronounced enough to be perceptible above the limits of accuracy that are present in climatic determinations on the basis of plant remains. The changes in distribution and composition of floras in western America during this time were in response to changes in precipitation rather than in temperature conditions.

If the Latah flora is older than the Mascall, it is pertinent to consider the route by which the element common to the Latah and the San Pablo floras migrated southward. It certainly did not move southeast of the rising mountains of western Oregon, since it does not appear in the Mascall. It may have extended along the Rocky Mountains, since certain elements of it are found in the Florissant beds. Recent work on this flora indicates that it is older than the Latah; if so, it scarcely belongs in this discussion. The flora may have found another path of migration west of the mountains, in the belt where rainfall was abundant all along the coast. The Weaver-ville flora furnishes some indication of this. Although it is older, it indicates the type of forest that should be found on the west side of the mountains. Being older, it represents a more tropical type of climate, with a number of genera now limited to low latitudes. Also, many of the leaves found in the flora are large and luxurious, indicating optimum conditions

¹ Chaney, R. W., The Succession and Distribution of Cenozoic Floras around the Northern Pacific Basin. Essays in Geobotany, p. 80, 1936. Univ. Calif. Press.

² Dorf, E., Carnegie Inst. Wash. Pub. No. 476, II, pp. 98-104, 1936.

of temperature and moisture. This is exemplified by the species of *Ilex* in the Weaverville and San Pablo floras, as I have suggested in the systematic portion of this paper. In addition to these, 6 species are common to the two floras. These make up 31 per cent of the San Pablo species, next to the largest proportion that occurs in another flora. Thus the Weaverville and the San Pablo have an element in common, the former having in addition a warmer element and the latter a temperate element. The Weaverville is considered to be older than the Bridge Creek.¹ Evaluating the differences in age and composition of the two floras, the Weaverville may be regarded as the southern limit of the *Taxodium-Nyssa* forest at the time when it still occupied a northern position, and the San Pablo as the northern limit of the same forest after it had migrated to its late Tertiary position. The path of this migration was probably along the west side of the mountains, since east of them a different flora is found. Unfortunately, no floras of intermediate age have been found along the assumed path of migration from the region west of the mountains, so this hypothesis is not supported by direct evidence. If such floras are found, they will probably show a close relationship to the *Taxodium-Nyssa* association as it is expressed in the Weaverville, the Latah, and the San Pablo floras.

Four species of the San Pablo flora occur in Eocene beds of western America, and compose not quite 2 per cent of that flora. This is a large proportion in view of the great difference in age. This is due to the climatic conditions of the San Pablo flora. It represents warm temperate conditions, and it is not unnatural that it will contain a few species that are more characteristic of subtropical than of temperate conditions. An added factor is that many Eocene floras are included in the comparison, so that diverse times and regions, with varied climates, are involved.

Summarizing the above paragraphs, the following statements may be made. The Weaverville flora, of older Oligocene age, represents the southern edge of the *Taxodium-Nyssa* forest. Cooling occurred, so that the flora migrated southward. At this time a portion of the flora extended eastward into the Latah region, and to a lesser extent was preserved in the Bridge Creek shales. Diastrophism of Middle Miocene times eliminated most of these remnants east of the mountains, resulting in the drier Upper Miocene Mascall flora. At about this same time, the northern edge of the *Taxodium-Nyssa* forest had come to occupy the region of San Francisco Bay. Further drying, and probably cooling, eliminated this flora from western America. A few species similar to the fossils occur in Mexico today; they may have arrived there by migrating down the west coast, or by invading Mexico from the Gulf region of the United States. Work now in progress on Miocene floras of southern California indicates that drying was more pronounced than in northern California, but that a few genera, such as *Persea* and *Magnolia*, existed in the southern coastal region.

¹ MacGinitie, H. D., Carnegie Inst. Wash. Pub. No. 465, 1937.

From the foregoing it is apparent that San Pablo species occur much more frequently in floras that are of pre-Pliocene age than in floras that are post-Miocene. The proportion is 26 to 4 counting actual occurrences, and 16 to 4 counting each species once regardless of in how many floras it occurs. No species in the San Pablo flora is restricted to Pliocene floras, and ten do not occur above the Miocene. The predominance of occurrences in older floras would be even greater if only floras from the same general climatic province were considered, since this would eliminate from the count two species in the Citronelle. This suggests a Miocene age for the San Pablo flora. As I have brought out in the section on climatic implications, the San Pablo flora grew in a climate in which summer precipitation was equal to winter precipitation. This is true of all pre-Pliocene floras of western America, and not true of any post-Miocene flora. All Pliocene floras now known definitely suggest a general decrease in rainfall, especially in summer. However, the Pliocene floras geographically close to the San Pablo are some distance removed from the base of the Pliocene. The Weiser flora, which is close to the base, is a long distance from the San Pablo, and probably was subject to different climatic conditions. Thus the climatic implications of the San Pablo flora also suggest a Miocene age. The history of the floras of western America, as I have outlined above, places the floras of earlier age and northern position in accordance with this determination. It is possible that climatic conditions typical of the Miocene, and consequently a flora typical of that epoch, may have persisted into basal Pliocene times. Climatic changes are probably not rapid, and may have persisted a short time after the appearance of new types of mammals considered to be typical of a later time. It is possible that the beds containing the flora discussed in this paper are transitional between the Miocene and the Pliocene. In any case, they are not far removed from the boundary between the two, and their allocation to one or the other epoch can be dependent upon the criteria used to determine that boundary.

THE GREEN VALLEY FLORULE

Recently, in a quarry from which abundant vertebrate remains are being taken, a few poorly preserved leaf impressions were collected by Chaney. This quarry lies on the south side of Mount Diablo, in the northeast quarter of the southwest quarter of Section 24, Township 1 South, Range 1 West, Mount Diablo Baseline and Meridian. It occurs in interbedded brown sands and gray shales, striking almost east-west and dipping north about 80°. The quarry is about 1000 feet stratigraphically higher than the upper contact of the Neroly, with evidences of one or more erosional unconformities in the intervening section. The formation in which it occurs was formerly called the Orindan, but on the basis of the vertebrates so far collected is considered to be somewhat younger, probably late Lower Pliocene. It is now tentatively named the Green Valley formation.

The leaf material at present consists of about 30 recognizable specimens, representing 5 or 6 genera as follows:

<i>Salix</i>	11 specimens
<i>Platanus</i>	7
<i>Populus</i>	5
<i>Alnus</i>	4
<i>Ulmus</i>	2
<i>Betula</i> (?)	1

Specific determinations are not warranted on the basis of the material so far collected, but the following remarks may be made concerning the relationships of these fossils:

The *Salix* resembles *S. coalingensis* Dorf¹ although somewhat smaller. This species is common in the California Pliocene, and is also present in the Pliocene deposits of the Great Plains.² It also resembles the San Pablo willow.

The *Populus* may be of two types, one like *P. emersoni* of the Neroly and *P. alexanderi* Dorf of the California Pliocene, and one like *P. plotremuloides* Axelrod.³ The leaves are generally smaller than the Neroly leaves, and the majority of them appear to represent the aspen type, with palmate bases.

The *Alnus*, and the *Betula*, if it is *Betula*, are too poorly represented to permit any reference to a species. The margins and tertiary venation are not preserved. The *Betula* is suggested by what appears to be a cordate base on one specimen.

The *Ulmus* is represented by two specimens, both of them small and with asymmetrical bases together with typical ulmaceous secondary venation. The margins are not preserved, but the size relates them to *U. brownellii* Lesqx. reported by Dorf from the California Pliocene, and *U. moorei* Chaney from the Pliocene of Beaver County, Oklahoma. *U. brownellii* was described from the John Day beds of Oregon. The leaves assigned to this species by Dorf are probably not the same as the Miocene material, but more likely represent a species limited to the Pliocene. In any case, this material is more closely related to the leaves from the Pliocene than to the leaves from the Miocene.

According to the above remarks, the specific relationships of these fossils is closer with the Pliocene floras of this region than with those of any other age. Most of the species mentioned are either limited to the Pliocene or most abundant at that time. Generic relationships are of course broader. All of the genera except *Ulmus* are present in the San Pablo flora, and other Miocene floras. All of them but the elm and the birch are still living in the immediate region, limited to stream courses and areas of con-

¹ Dorf, E., Carnegie Inst. Wash. Pub. No. 412, 1933.

² Chaney, R. W., and Elias, M. K., Carnegie Inst. Wash. Pub. No. 476, I, 1936.

³ Axelrod, D. I., Carnegie Inst. Wash. Pub. No. 476, III, p. 169, pl. 4, figs. 1-3, 1937.

tinuously moist soil. Presumably they required the same conditions in the past. Their presence in the Green Valley beds is consistent with the view that regards these beds as stream deposits. The absence, even in such a small collection as this, of other genera of the San Pablo is also significant. If there had been present in this flora any of the species typical of the Miocene floras of California, such as *Taxodium*, *Nyssa*, *Persea*, or *Juglans*, these should have appeared in the collection. Their absence, together with the consistent representation of stream border types only, is strong evidence that dry summer conditions were inaugurated in this region between the deposition of the Neroly and the Green Valley. In other words, the boundary between the Miocene and the Pliocene occurs between these two formations, according to the method of determining the boundary used in connection with fossil floras. This evidence and the conclusions drawn from it are in accord with the conclusions stated before this flora was known.

CONCLUSIONS

1. The San Pablo flora, collected from the upper member of the San Pablo Group, consists of 26 species, 4 of which are specifically indeterminable on the basis of material now at hand.
2. The flora is most similar to the present *Taxodium* forest of the southeastern United States, especially at its northern border.
3. The climate indicated by the flora was probably one of only slightly increased temperature over that prevailing in the region today, with a greatly increased rainfall evenly distributed over the year.
4. The age of the leaf-bearing beds of the upper member (Neroly) of the San Pablo Group is probably Upper Miocene, on the basis of the specific content of the flora and of the climate indicated. Both of these characters of the flora show a close similarity to typical Miocene floras and conditions, and a wide dissimilarity from typical Pliocene floras and conditions on the west coast of North America.
5. The flora supports the theory that there was a progressive migration southward of temperate floras in western America from high latitudes in the Eocene.

SYSTEMATIC DESCRIPTIONS

PHYLUM PTERIDOPHYTA

ORDER EQUISETALES

Family EQUISETACEÆ

Genus EQUISETUM Linné

Equisetum sp.

Twenty-three specimens of this plant have been collected from the San Pablo beds, including both aerial stems and rhizomes.

Description—Aerial stems of short fragments up to 3 centimeters long, diameters from 5 to 7 millimeters. Hollow, filled with sedimentary material,

the plant tissue represented by a thin carbonaceous film. Twelve to fifteen longitudinal ridges are more or less distinctly preserved on the impressions. One specimen shows an unmistakable node, marked by a transverse ridge with transverse grooves immediately above and below it. The longitudinal ridges appear to continue across the nodal ridge. The node bears the base of a branch springing from one wall of the transverse ridge; this branch has an enlarged circular base tapering rapidly outward, and marked at the joint with the stem by a groove suggesting an abscissal layer.

Discussion—The absence of critical characters in these fossil remains of the genus *Equisetum*, and the consequent lack of climatic and stratigraphic value makes it improper to dignify the material with a specific name. It is to be noted, however, that the fossils resemble, among other species, the living *E. arvense* L., which is widely distributed in temperate regions and includes in its geographic range the area in which most of the living equivalents of the San Pablo plant species are found. It inhabits moist places along streams and pools.

Occurrence—Loma Ranch, Loc. 607; Bailey Road, Loc. 618; Altamont Pass, Loc. 199.

Collection—Univ. Calif. Mus. Pal., No. 1135.

PHYLUM SPERMATOPHYTA

CLASS GYMNOSPERMÆ

ORDER CONIFERALES

Family TAXODIACEÆ

Genus TAXODIUM Rich.

Taxodium dubium Heer

(Plate 3, figs. 1, 2, 4a)

Taxodium dubium Heer, Fl. Tert. Helv., vol. 1, p. 49, pl. 17, figs. 5-15, 1855.

Numerous specimens of this plant, for the most part leafy twigs, have been collected from the San Pablo localities. Lesquereux identified similar material from Corral Hollow as *Sequoia angustifolia*, but more complete material leads me to change this reference. *Taxodium* leaves are commonly smaller and more slender than those of *Sequoia*. Large leaves of the former may be equal to small leaves of the latter, but in both cases these are not typical. The size range of the fossils matches that of *Taxodium* more nearly than that of *Sequoia*. The base of the twigs in *Sequoia* is sheathed by small scale-like leaves which are generally absent in *Taxodium*. These are also lacking in the fossils. Furthermore, cone scales have been collected which are identical with cone scales of *Taxodium distichum* Rich. Since no evidence of *Sequoia* aside from doubtful foliage has as yet been found, and ecological considerations strongly support the presence of *Taxodium* rather than *Sequoia* in this flora, it is considered justifiable to change Lesquereux's identification of these remains. *Taxodium* was certainly present in this flora, and while *Sequoia* may have been, a definite statement to that effect must await more conclusive evidence. *Taxodium* is today distributed along the coastal plain from Texas to Delaware, and up the Mississippi Valley to Indiana. One species occurs in Mexico.

Occurrence—Loma Ranch, Loc. 607; Corral Hollow, Loc. P361.

Collection—Univ. Calif. Mus. Pal., Plesiotypes, Nos. 1137, 1138, 1285; Nos. 1136, 1139.

Family TAXACEÆ**Genus TAXITES Brong.*****Taxites olriki* (?) Heer**

Taxites olriki Heer, Fl. Foss. Arct., vol. 1, p. 95, pl. 1, figs. 21-24c, pl. 45, fig. 1a, b, c, 1868; vol. 2, Abt. 2, p. 23, pl. 1, fig. 8, pl. 2, fig. 5b, 1871.

Lesquereux reported one specimen of *Taxites* from the Corral Hollow beds, the only one so far found in San Pablo collections. The specimen is in the collections of the University of California, where I have had an opportunity to examine it. There seems to be no question about its closer relationship to *Taxus* than to any other gymnosperm genus. The foliage resembles *T. brevifolia* Nuttall of western United States and *T. floridana* Chapman of Florida. The size of the needles suggests a closer relationship to the California species than to the Florida species. The rarity of specimens in the collections suggests that it was scarce in the forests of Neroly time. It was probably then, as now, a relict species in the California flora, a remnant of a genus that was more abundant and widespread in earlier times.

Occurrence—Corral Hollow, locality unknown.

Collection—Univ. Calif. Mus. Pal., Plesiotype, No. 1286.

CLASS ANGIOSPERMÆ**Subclass MONOCOTYLEDONÆ****ORDER PANDANALES****Family TYPHACEÆ****Genus TYPHA Linné*****Typha* sp.**

Ten fragments of *Typha* leaves have been collected from the San Pablo localities. None of them have specifically diagnostic characters, and since this genus is little more than a form genus, it is the writer's opinion that fossils do not merit a specific name. No stratigraphic conclusions are supported by the presence of these fossils, and the only ecologic one is that the site of deposition was in or near an area of swamps or slow-moving streams.

Occurrence—Loma Ranch, Locality 607; Bailey Road, Locality 618.

Collection—Univ. Calif. Mus. Pal., Nos. 1140, 1141.

ORDER GRAMINALES**Family GRAMINEÆ****Genus POACITES Brong.*****Poacites* sp.**

Fifty-four fragments in the San Pablo collections have been referred to this genus. They range up to 11 centimeters long, with both the base and apex missing, and from 4 to 7 millimeters wide. They are parallel-veined, with a prominent midrib marked by a strong longitudinal fold. Occasional specimens show the fragments arranged as if they sprang radially from a single point, or perhaps pinnately from a stalk. I have been able to discern no diagnostic characters in these fossils, and so have assigned no specific name to them. It is impossible to relate them to any single living plant,

although they are obviously some kind of grass. The abundance of the material suggests that the fossils represent a water-living or moist-ground type, rather than a grass which occupied the drier uplands, although this latter alternative is not impossible.

Lesquereux identified *Geonomites schimperi*¹ from Contra Costa on the basis of a specimen that he rightly said was too small and fragmentary for positive identification. While palms are not wholly unexpected in this flora, their climatic requirements are sufficiently different to require strong evidence before accepting them as members of the San Pablo flora. I have been unable to find the specimen from which the drawing was made, and have found no specimens in more recent collections that resemble palms. Many of the specimens of *Poacites* appear to have connate rays, such as Lesquereux attributed to his *Geonomites*, but careful examination shows them to be separate grass blades. This leads me to suspect the accuracy of the drawing in Lesquereux's paper, and deny the presence of *Geonomites* in this flora until more precise evidence is forthcoming.

Occurrence—Loma Ranch, Locality 607; Bailey Road, Locality 618; Altamont Pass, Locality 199; Corral Hollow, Locality P361.

Collection—Univ. Calif. Mus. Pal., Nos. 1142, 1143.

ORDER LILIALES

Family LILIACEÆ

Genus SMILAX Linné

Smilax diforma n. sp.

(Plate 3, figs. 4b, 5)

Description—Leaves of two types, broad and narrow. The broad type is round, tip missing, base cordate, length preserved 8 centimeters, probably 10 to 12 centimeters when complete, width preserved 8 centimeters, probably 9 to 11 in life. Petiole missing, nervation palmate, midrib only slightly more prominent than the lateral veins, slightly curved, thick for the full distance the impression is preserved. Lateral ribs four in number, the inner pair prominent and the outer pair faint; the inner pair begin to recurve toward the midrib below the upper limit of the impression, and the outer pair become obscure halfway up the leaf. Secondary veins obscure, apparently irregularly reticulate, tertiary veins not preserved. Margin not preserved. Texture apparently fleshy, indicated by the wrinkled impression. Narrow leaves lanceolate, tip acuminate, base cuneate, length 9 centimeters, width 4 centimeters. Petiole missing. Nervation palmate, the midrib prominent, extending to the apex of the leaf. Lateral veins two, less prominent than the midrib, continuous to the apex where they almost rejoin the midrib. Secondaries obscure, apparently irregularly reticulate within the lateral veins and camptodrome outside of them. Tertiaries not discernible. Margin entire, texture thick and fleshy.

Discussion—This material is clearly distinct from any fossil *Smilax* hitherto described. *S. goshenensis* Chaney and Sanborn² is similar, but is separated by the characters of the secondary veins and the shape, as well as its small size. *S. lamarensis* Knowlton found in several Tertiary deposits is superficially similar, but is different in many minor characters.

¹ U. S. Geol. Surv. Terr. Rept., vol. 8, p. 241, pl. 50, fig. 9, 1883.

² Chaney and Sanborn, Carnegie Inst. Wash. Pub. No. 439, p. 64, 1933.

The only similar modern species of this genus with which the writer is acquainted is *S. rotundifolia* L. of the southeastern United States. Other species, such as *S. walterii* Pursh. and *S. mexicana* Griseb., agree with the fossils in regard to one leaf type only; not to both types. *S. rotundifolia* occupies woods and swamps in the eastern part of North America, extending as far north as southern Canada.

The leaves identified as *Cinnamomum affine* by Lesquereux from Corral Hollow probably represent narrow leaves of *Smilax*. Their characters as illustrated in volumes 7 and 8 of the Reports of the United States Survey of the Territories show no disagreement with either my specimens or modern leaves of *Smilax*; also, *Cinnamomum* is a genus that would scarcely be found in association with the San Pablo flora, being limited today to the Indo-Malayan region.

Occurrence—Loma Ranch, Locality 607.

Collection—Univ. Calif. Mus. Pal., Cotypes, Nos. 1144, 1145.

Subclass DICOTYLEDONÆ

ORDER SALICALES

Family SALICACEÆ

Genus SALIX Linné

Salix sp.

Salix integra? Goeppert and *S. varians* Goeppert have both been reported from the San Pablo beds by Lesquereux and Knowlton. In view of the fact that these are European species, and that the evidence that a single species of this genus included that continent and this one within its range is inconclusive, it is thought better to abandon these names for these fossils. The material available to me is entirely fragmentary, although the pieces usually show the details of venation quite distinctly. Identification of willow leaves is unsatisfactory unless complete material is at hand, since leaves of different species of willows are separable only by minor characters. Thus, the fragments of *Salix* leaves in the San Pablo collection resemble the modern *S. lasiolepis* Benth., *S. lasiandra* Benth., and *S. lævigata* Bebb almost as well as they do *S. nigra* Marsh and *S. longipes* Anders. The first three are western species, the last two are common in the southeastern states along the borders of streams and swamps. The narrow and broad types of leaves among the fossils are matched by leaves from either of the two eastern species. It is considered inadvisable, therefore, to apply a specific name to these fossils until more definitive material is available.

Occurrence—Loma Ranch, Locality 607; Bailey Road, Locality 618; Altamont Pass, Locality 199.

Collection—Univ. Calif. Mus. Pal., Nos. 1146, 1147, 1148, 1149.

Genus POPULUS Linné

Populus balsamoides Goeppert

(Plate 4, fig. 3, plate 5, fig. 3)

Populus balsamoides Goeppert. F. A. Heer, Fl. Foss. Arct., vol. 2, Abt. 2, p. 26, pl. 2, fig. 3, 1871.

Seventy-three leaves or fragments of leaves represent this species in the San Pablo collections, some of them very excellently preserved. This condition is to be expected in view of the habitat and leaf-shedding character

of this genus. Lesquereux noted this species and I have collected it from all four localities. Comparison with leaves of modern trees suggests that these fossils should more properly be related to *P. grandidentata* Michx., which grows in moist ground near the borders of swamps and streams from Nova Scotia to Pennsylvania and Kentucky. A variety with more ovate acuminate leaves extends the range of this species to North Carolina and Virginia.

Occurrence—Loma Ranch, Locality 607; Bailey Road, Locality 618; Altamont Pass, Locality 199; Corral Hollow, Locality P361.

Collections—Univ. Calif. Mus. Pal., Plesiotypes, Nos. 1236, 1237.

Populus emersoni n. sp.

(Plate 4, figs. 1, 2)

Description—Shape ovate, rarely lanceolate-ovate; apex acute or acuminate; base truncate, commonly with subordinate cuneate portion near the petiole; length from 4 to 7 centimeters, rarely 10 centimeters, width from 3 to 5 centimeters, rarely 7 centimeters; petiole preserved on one specimen 2.5 centimeters; midrib continuous to apex, straight except at the distal portion which becomes slightly sinuous; secondaries five to nine pairs, leaving midrib at angles of 40° to 50°, opposite to sub-opposite with occasional alternate veins, camptodrome, curving upward distally and splitting into several branches which loop to join the secondary next above; tertiary veins irregularly percurrent, nervules reticulate; margin shallowly crenate or finely serrate; texture thin.

Discussion—These leaves show a close resemblance to *Populus trichocarpa* T. and G., now living on the west coast of America, especially in the higher latitudes and altitudes, and to the fossil species *P. alexanderi* Dorf from the Pliocene of California, and *P. eotremuloides* Knowlton from the Payette and Mascall floras. *P. trichocarpa* is considered to be its living equivalent.

Two parallel lines of poplars are present in the later Tertiary deposits of western America. These begin with *Populus eotremuloides* Knowlton and *P. lindgreni* Knowlton from the Payette, 49 Camp, Trout Creek, and other Upper Miocene floras. *P. lindgreni* is apparently the first representative of the line that has resulted in the aspen group, that is, *P. tremuloides*, *P. aurea*, and *P. grandidentata*. This group is represented in the San Pablo flora by *P. balsamoides*. The *balsamoides-grandidentata* line appears to be the type that grow in milder situations, while the *tremuloides-aurea* line represents the types that grow under more severe conditions. Both of these lines in the aspen group are represented in fossil floras. The *balsamoides-grandidentata* type is seen in specimens Nos. 561 and 562 from Trout Creek, 661 from Blue Mountains, and 956 from 49 Camp. All of these floras are of the milder, more humid type. The *tremuloides-aurea* type is seen in *P. plotremuloides* Axelrod from the Mount Eden flora¹ and *P. irvingi* Chaney from the Deschutes flora.² Both of these floras are of the drier or colder type. The *lindgreni-grandidentata-tremuloides* group is separable from the *eotremuloides-trichocarpa* group by the following characters: a tendency toward the development of large remote recurved teeth, especially in the *grandidentata* line; small size in the *tremuloides* line; a consistent ovate shape; a palmate arrangement of the secondaries with the

¹ Axelrod, D., Carnegie Inst. Wash. Pub. No. 476, III, p. 169, pl. 4, figs. 1, 2, 3, 1937.

² Chaney, R. W., Carnegie Inst. Wash. Pub. No. 476, IV, p. 216, pl. 7, figs. 3, 4, 1938.

development of a gap between the lower pair of secondaries and the next higher pair. The last character appears to be the most consistently true.

The other line of late Tertiary poplars in western America is the *eotremuloides-trichocarpa* group. MacGinitie¹ has already pointed out the confusion in the naming of Knowlton's species from the Payette, which should apparently have had the names interchanged. This group is marked by a more lanceolate shape, especially prominent in the later forms, smaller more numerous teeth, and a definite tendency toward a pinnate arrangement of the secondary veins. Even in those leaves that at first appear to be palmate there is no large gap between the lowest and the next highest set of secondaries, thus these retain a truly pinnate aspect. The Blue Mountains species, identified by Oliver as *P. lindgreni*, appear to be more than one species. No. 661 is truly an aspen; No. 662, in shape, margin, and the pinnate arrangement of the secondaries, has much closer affinities with the *eotremuloides-trichocarpa* group. No. 663 also appears to have affinities with this line, although the relationship is not quite so clear as in No. 662. In No. 663 a gap appears between the two lowest strongly marked sets of secondaries, but a faint pair is present in this gap. The presence of this faint pair, together with the longer shape and the fine close-set teeth, give it a closer resemblance to the *eotremuloides-trichocarpa* group than to the *lindgreni-grandidentata* group. Whether or not No. 663 is an aspen, No. 662 is clearly not one, and represents another occurrence of the second line of poplars in the Tertiary deposits.

The next expressions of this line are in *P. emersoni* of this flora, followed by *P. alexanderi* Dorf from the California Pliocene, and the modern *P. trichocarpa*. It is interesting to note the development of the long acuminate leaves in this phylad through time. Only one leaf out of almost sixty specimens in the San Pablo flora is long. In the Pliocene form one leaf out of six specimens is long. In the modern form many leaves, perhaps the majority of them, are long. Apparently a tendency toward long and relatively narrow leaves has become more and more commonly expressed since upper Miocene times. What relation, if any, this tendency has with climatic requirements of the tree is obscure. The modern *P. trichocarpa* appears to survive somewhat less genial conditions than are indicated for its Upper Miocene ancestor.

Populus emersoni is named in honor of Dr. M. L. Emerson of Oakland, California, who has contributed some excellent specimens from Locality 618.

Occurrence—Loma Ranch, Locality 607; Bailey Road, Locality 618; Altamont Pass, Locality 199; Corral Hollow, Locality P361.

Collection—Univ. Calif. Mus. Pal., Cotypes, Nos. 1238, 1239, 1240, 1241.

ORDER MYRICALES

Family MYRICACEÆ

Genus MYRICA Linné

Myrica diforme (Sternberg) Chaney

(Plate 4, fig. 4)

Myrica diforme (Berry) Chaney, Carnegie Inst. Wash. Pub. No. 346, p. 103, pl. 9, figs. 1, 3, 5, 1927.

Two specimens, one with its counterpart, have been collected from the San Pablo localities, but the characters of these leaves are sufficiently dis-

¹ MacGinitie, H. D., Carnegie Inst. Wash. Pub. No. 416, II, p. 49, 1933.

tinct to make their identification certain. The fossils superficially resemble *Lyonothamus floribundis* Gray, but the shape of the base clearly separates them from this genus. Chaney has referred this fossil *Myrica* to *M. asplenifolia* Linné. The San Pablo fossils are also most closely matched by this living species.

Occurrence—Bailey Road, Locality 618.

Collection—Univ. Calif. Mus. Pal., Plesiotype, No. 1242.

ORDER JUGLANDALES

Family JUGLANDACEÆ

Genus JUGLANS Linné

Juglans oregoniana Lesqx.

Juglans oregoniana Lesquereux, Mus. Comp. Zool. Mem., vol. 6, p. 35, pl. 9, fig. 10, 1878.

Carya egregia (Lesqx.) LaMotte (in part), Carnegie Inst. Wash. Pub. No. 455, V, p. 116, 1936 (*Juglans oregoniana* in synonymy only).

This species is abundantly represented by leaves and fragments of them from the San Pablo localities. LaMotte in his discussion of the Cedarville flora removed *Juglans oregoniana* to the genus *Carya*. There are some more or less constant characters that serve to separate these genera. *Carya* leaflets are fewer in number than those of *Juglans*, and tend almost always to become larger toward the distal end of the leaf, while *Juglans* leaflets show a less pronounced tendency to become smaller distally. These characters are of course useful only when a complete leaf is preserved, as in the Cedarville material; they are of small value when only separate leaflets are preserved, as in the San Pablo material. *Carya* leaflets are obovate in shape, with a cuneate base except rarely on small basal leaflets. *Juglans* leaflets are lanceolate, with truncate or cordate bases, especially in the species to which *J. oregoniana* has been referred. The typical bases of these leaflets are reflected in the reverse curves of the lower secondaries. In *Carya* the secondary veins are usually craspedodrome, and appear dichotomous owing to prominent branches issuing from their distal portions. These characters are largely suppressed in *Juglans*, in which the secondaries are regularly camptodrome and without prominent branches.

The San Pablo fossils, Lesquereux's figure, and the specimens from Trout Creek¹ all possess the *Juglans* characters and none of them show any of the typical *Carya* characters. LaMotte points out that terminal leaflets of *Carya* are distinct from lateral leaflets, and occur in the Cedarville flora in the proportion of about one terminal to four lateral leaflets. In the San Pablo material at least, there is no indication among the many specimens of clearly marked terminal leaflets, such as would be expected if these were *Carya*. It is unquestionable that *Carya* was present in the Cedarville flora, but in view of the much closer relationship of the San Pablo material to *J. nigra* than to any species of *Carya* in the University of California Herbarium, I cannot believe that *Juglans oregoniana* properly belongs in that genus.

Juglans nigra is distributed throughout the middle western United States in richer soils of bottomlands and hillsides. Although it is present east of the Alleghany Mountains, it is rarer in that region.

Occurrence—Loma Ranch, Locality 607; Altamont Pass, Locality 199.

Collection—Univ. Calif. Mus. Pal., No. 1243.

¹ Carnegie Inst. Wash. Pub. No. 416, II, 1933.

ORDER FAGALES

Family FAGACEÆ

Genus CASTANEA Anderson

Castanea castaneæfolia Knowlton

Castanea castaneæfolia (Heer) Knowlton, U. S. Geol. Surv. Bull. 152, p. 60, 1898;
Castanea ungeri Heer, Lesquereux, U. S. Geol. Surv. Terr. Rept., vol. 8, p. 246,
 pl. 52, figs. 1, 3, 4, 6, 7, 1883.

Only one specimen and its counterpart have been found in the San Pablo beds. Nevertheless, the characters are sufficient to make its relationships clear. It is closely related to *C. pumila* Mill., which usually grows upon the uplands away from streams and areas of deposition in the southeastern part of the United States. *C. castaneæfolia* probably occupied a similar habitat; this is indicated by paucity of its leaves in the collections. Lesquereux identified a broad chestnut-like leaf from Corral Hollow as *Castanea ungeri*. This is discussed below under the genus *Tetracera*.

Occurrence—Loma Ranch, Locality 607.

Collection—Univ. Calif. Mus. Pal., No. 1252.

Family BETULACEÆ

Genus ALNUS Linné

Alnus corrallina Lesqx.

(Plate 6, figs. 4, 5)

Alnus corrallina Lesquereux, U. S. Geol. Surv. Terr. Rept., vol. 8, p. 243, pl. 51, figs. 1-3, 1883. Brown, R. W., U. S. Geol. Surv. Prof. Paper 186-J, p. 170, pl. 48, figs. 1-3, 1937.

In the collections made by Lesquereux from Corral Hollow are a number of leaves to which he applied the name *Alnus corrallina*. This generic reference is substantiated by the presence of a pistillate ament which he figured with the leaves. Lesquereux pointed out the resemblance of this fossil species to the living *A. viridis* (Chaix) DC., which is now synonymized with *A. alnobetula* (Ehrh.) K. Koch.; it is also closely similar to *A. rhombifolia* Nuttall, which is widely distributed along streams in the Coast Ranges, within a few miles of the fossil localities.

In the collections that are the subject of the present study there are numerous betulaceous leaves, some of which are clearly referable to Lesquereux's species, and some that are distinctly different. The latter are exactly matched by *Betula multinervis* Jennings in the fossil flora of Missoula, Montana. Jennings has figured a pistillate ament which he considers to represent *Betula*, and to corroborate the evidence of the leaves that this genus was present. A more complete birch catkin, collected at Missoula by Chaney in 1920, is figured in plate 6. I agree with Jennings that *Betula multinervis* closely resembles the living *B. lenta* Linné, now living in eastern United States. Some of my fossils do not clearly match these species of *Alnus* and *Betula*, partly because of incomplete preservation, and partly because the leaf characters of these genera overlap. A careful examination of herbarium material reveals that some characters nearly always serve to separate *A. rhombifolia* and *B. lenta*. These are: *B. lenta* leaves have larger, more finely pointed, and more numerous teeth than *A. rhombifolia*—these points are uniformly present in the fossils I consider to be birches, although they are so fine that they usually break off in the process of cleaning the margins; the bases of *B. lenta* are cordate or

sub-cordate, whereas *A. rhombifolia* bases are cuneate or at most truncate; the basal secondary veins of *B. lenta* are concave upward, while in *A. rhombifolia* they show a reverse curve near the midrib. These characters of the basal secondaries are a reflection of the type of bases in each species. Moreover, the upper secondaries in *Betula lenta* are usually straight, whereas in *Alnus rhombifolia* they are usually concave toward the apex, as well as being more remotely spaced. Another character that is only occasionally discernible in fossil leaves is that the tertiaries in *Betula* are numerous, relatively straight, and of equal thickness throughout their length, whereas in *Alnus* they are less numerous, less straight, and usually fade out somewhat in the area between the secondaries.

Characters of this sort are not entirely satisfactory bases for separating some of the leaves from *A. corrallina* and designating them as *B. multinervis*. However, a distinction between leaves of alder and birch was made by Jennings in the Missoula flora, and Brown has recently determined that the Missoula alder is *A. corrallina*.¹ *Alnus rhombifolia* is at present distributed from Idaho and eastern Washington southward through the Coast Ranges and the western slope of the Sierra Nevada to southern California. It grows best along streams or elsewhere where the soil is moist throughout the year, in company with California sycamore, Oregon ash, and western dogwood.

Occurrence—Loma Ranch, Locality 607; Bailey Road, Locality 618; Altamont Pass, Locality 199.

Collection—Univ. Calif. Mus. Pal., Plesiotypes, Nos. 1244, 1245, 1246, 1247.

Genus BETULA Linné

Betula multinervis Jennings

(Plate 6, figs. 2, 3)

Betula multinervis Jennings, Mem. Carnegie Mus., vol. 8, No. 2, p. 411, pl. 24, fig. 4, pl. 27, figs. 1, 1a, 1b, 1c, 2, pl. 28, fig. 2. 1920.

The reasons for separating this species from *Alnus corrallina* are set forth above. In addition, species in two other genera are possibly descendants of the plant that possessed these leaves, both on ecological and morphological grounds. These are *Ostrya virginiana* K. Koch, and *Carpinus caroliniana* Walt. The reasons for calling the fossils *Betula* rather than one of these genera were primarily the close match to leaves from Missoula that are associated with *Betula* fruiting material, plus the following characters noticed in careful examination of modern material:

Betula lenta leaves differ from *Ostrya virginiana* leaves by having less prominent teeth and smaller, fewer branches from the distal portions of the secondaries. Moreover, *B. lenta* leaves show tertiary veins that are almost always truly percurrent, whereas in *Ostrya* they spring from the secondaries alternately and are joined by obscure irregular veinlets that are roughly parallel to the secondaries.

Betula lenta leaves differ from *Carpinus caroliniana* leaves by their smaller size, and the arrangement of their tertiary veins. In *Betula*, the tertiaries tend to become less percurrent near the midrib, and more concentric about the point of juncture of the midrib and the secondaries than

¹ Brown, R. W., U. S. Geol. Surv. Prof. Paper 186-J, p. 170, 1937.

is the case in *Carpinus*. Furthermore, in *Carpinus* the secondaries often branch near the margin, with the upper branch bending up sharply at the point of branching, which gives the appearance of dichotomy to these veins. This is not true of *Betula*, in which the secondaries continue in the same line past the point of branching.

These characters seem to be constant on the basis of the limited material available to me in the Herbarium of the University of California. They may not be found to be consistently true when abundant material is examined. In any case, the characters are minor, and not wholly satisfactory for either generic or specific determination. The fact that these species are both living with the majority of the descendants of the San Pablo species suggests that either they or their ancestors were present in the fossil flora. Both genera are represented in older floras to the north. But with the fossil material now at hand, I can find no reason for including them in this flora. Future collections may obtain material that more definitely suggests their presence; if so, the ecological conclusions of this study will be further supported.

University of California Herbarium sheets 119239 and 480336 of *Betula lenta* resemble the fossils in all particulars. Sheet 280334, labeled *B. allegheniensis* Britton, is also an excellent match. Some authorities consider this species to be the same as *B. lenta*. This species is distributed along the eastern coast of North America from Newfoundland to the Chesapeake Bay, west to Iowa, and south along the Appalachian uplands almost to the Gulf of Mexico. It attains its best development on well drained slopes that receive abundant moisture.

Occurrence—Loma Ranch, Locality 607; Bailey Road, Locality 618; Altamont Pass, Locality 199.

Collection—Univ. Calif. Mus. Pal., Plesiotypes, Nos. 1248, 1249, 1250, 1251.

ORDER RANALES

Family MAGNOLIACEÆ

Genus MAGNOLIA Linné

Magnolia californica Lesqx.

Magnolia californica Lesquereux, Mus. Comp. Zool. Mem., vol. 6, No. 2, pl. 6, figs. 6, 7, 1878.

Four specimens of this species have been collected from the San Pablo localities. None of these is complete. There has also been collected a fossil that may represent part of the fruiting structure of a magnolia, although the preservation is too poor to permit definite identification. All of the preserved characters of the leaves are the same as the Chalk Bluff species.

The most similar living species is *Magnolia grandiflora* L., according to the material available to me. The fossil species has been referred by others to *M. cordata* Michx. and *M. acuminata* L. All three species grow today in association with other living relatives of the San Pablo species in the southeastern states. Sargent states that *M. grandiflora* occupies rich moist soil at the borders of swamps and ponds, or rarely on rolling hills.

Occurrence—Loma Ranch, Locality 607; Bailey Road, Locality 618; Corral Hollow, Locality P361.

Collection—Univ. Calif. Mus. Pal., Nos. 1253, 1254.

Family LAURACEÆ

Genus PERSEA Plum.

Persea princeps Schimper

(Plate 7, figs. 1, 2)

Persea princeps Schimper, Pal. Veget., vol. 2, p. 831, 1870-1872.*Laurus princeps* Heer, Fl. Tert. Helv., vol. 2, p. 77, pl. 89, figs. 16, 17, pl. 90, figs. 17, 20, pl. 97, fig. 1, 1856.*Laurus californica* Lesquereux, U. S. Geol. Surv. Terr. Rept., vol. 8, p. 252, pl. 57, fig. 3, pl. 58, figs. 6-8, 1883.*Laurus grandis* Lesquereux, *ibid.*, p. 251, pl. 58, figs. 1, 3.*Laurus salicifolia* Lesquereux, *ibid.*, p. 251, pl. 58, figs. 4, 5.*Persea pseudo-carolinensis* Lesqx., Mus. Comp. Zool. Mem., vol. 6, No. 2, p. 19, pl. 7, figs. 1, 2, 1878; Knowlton, U. S. Geol. Surv. Mon. 32, pt. 2, p. 725, pl. 95, fig. 4, 1899; MacGinitie, Carnegie Inst. Wash. Pub. No. 465, III, p. 139, 1937.

Lesquereux described three species of *Laurus* from Corral Hollow and noted one previously described species. Inasmuch as "*Laurus*" was used at that time as little more than a form genus, a critical study of the fossils and a careful comparison of them with leaves of modern lauraceous leaves was pursued in an attempt to arrive at a more accurate determination of the fossils' affinities.

There are numerous specimens of these leaves in the San Pablo collections. Many of them are fragmentary, but usually there is sufficiently good material to permit accurate identification. It was found that all of the fossils are matched by leaves of *Persea borbonia* Spreng. This species possesses both pinnate leaves and those that appear to be palmate owing to the development and isolation of the lower pair of secondaries. The entire variation among the four species identified by Lesquereux is covered by the leaves of the modern species. I can see no justification for separating the fossils into more than one species. *Persea pseudo-carolinensis* Lesquereux has been related to *P. borbonia* (*P. carolinensis* Nee) and is probably the same species as the one under discussion here. *Persea princeps* is the oldest name referring this species to the modern genus which it most closely resembles, so this determination made by Schimper has been retained.

It should be noted that *Phœbe hartwegii* Meissn. of Mexico is also very similar to the fossils, although generally of smaller size and differing in minor characters of the vegetation. This species was originally described as *Persea hartwegii*, and may be a more or less distantly related descendant of that fossil form. *Persea borbonia* inhabits rich moist soil along streams and swamps within the range of *Taxodium distichum*, rarely extending as far north as the bald cypress does.

Occurrence—Loma Ranch, Locality 607; Bailey Road, Locality 618; Altamont Pass, Locality 199; Corral Hollow, Locality P361.

Collection—Univ. Calif. Mus. Pal., Plesiotypes, Nos. 1255, 1256; Nos. 1257, 1258.

Genus UMBELLULARIA Nutt.

Umbellularia oregonensis Chaney*Umbellularia oregonensis* Chaney, Carnegie Inst. Wash. Pub. No. 349, IV, pp. 59-62, pl. 1, figs. 1, 3, 5, 7, 1925.

Two small leaves are the only record of this genus yet obtained from the San Pablo localities. One of them is poorly preserved in a rather coarse matrix, so that little but the outline of the leaf remains, while the other

shows venation that suggests it belongs to this genus. The fossils resemble the living *U. californica* Nutt. and the fossil *U. lanceolata* Berry.¹ The only difference between *U. lanceolata* and *U. oregonensis* seems to be the smaller size of the former. The living *U. californica* commonly has leaves as small as *U. lanceolata*.

This species is not to be expected in association with the other San Pablo species. The rarity of the leaves collected indicates that it was not abundant in the flora; possibly a few trees existed as outliers to their normal range, which at San Pablo time was farther north and farther inland, where their leaves are found preserved in large numbers.

The modern *Umbellularia* and *Persea* are closely related, as indicated by both their leaves and fruiting structures, and it is possible that in the Miocene one species was present that was ancestral to both genera. It is at least true that fossil leaves of the two genera are difficult to distinguish from each other. In most cases, *Persea* leaves are more prominently palmate owing to the greater development of the lower pair of secondaries, while *Umbellularia* leaves are, as far as I know, never actually palmate except for the development of a pair of small marginal secondaries close to the base of the leaf. However, not all *Persea* leaves are palmate, and often the basal secondaries are indistinguishable in fossils assigned to *Umbellularia*. While *Umbellularia* leaves often are as large as *Persea*, they more frequently are considerably smaller and usually narrower than any *Persea* leaves noted in the University of California Herbarium. These characters are the basis for separating the two genera in this discussion.

Occurrence—Bailey Road, Locality 618.

Collection—Univ. Calif. Mus. Pal., Nos. 1259, 1260.

ORDER ROSALES

Family PLATANACEÆ

Genus PLATANUS Linné

Platanus dissecta Lesqx.

Platanus dissecta Lesquereux, Mus. Comp. Zool. Mem., vol. 6, no. 2, p. 13, pl. 7, fig. 12, pl. 10, figs. 4, 5, 1878.

This species is represented by twenty-seven impressions of leaves in San Pablo collections. As mentioned above, many more impressions were seen on the hanging wall of the small prospect tunnel at Locality 607. This indicates that sycamore leaves were more numerous in the deposits than the leaf count indicates. Possibly at this particular place a small pool was overhung by a sycamore tree which contributed its leaves copiously to the sediments. Some impressions collected from the San Pablo beds appear to represent flakes of bark that are so commonly shed by species of *Platanus*.

Plananus dissecta has been observed in many Tertiary floras in western America. It has repeatedly been referred to the living *Platanus occidentalis* L., a reference with which the writer agrees. *P. occidentalis* grows in the southeastern states, extending west to the Great Plains, and north to Canada. It reaches its best development in the Ohio and Mississippi River valleys where it abundantly grows along streams and in rich bottoms. The leaves are substantial and capable of transport over considerable distance before destruction, and fragments are easily identifiable, all of which are probable factors in their abundance in the record.

¹ Berry, U. S. Geol. Surv. Prof. Paper 154-H, p. 260, pl. 59, fig. 1, 1929.

Occurrence—Loma Ranch, Locality 607; Bailey Road, Locality 618; Altamont Pass, Locality 199; Corral Hollow, Locality P361.

Collection—Univ. Calif. Mus. Pal., Nos. 1261, 1262, 1263.

Family ROSACEÆ

Genus PRUNUS Linné

Prunus chaneyi n. sp.

(Plate 5, figs. 4, 5)

Description—Leaves obovate; apex blunt; base round; slightly inequilateral; length 5 to 6 centimeters; width 2 to 3 centimeters; petiole straight, 7 to 9 millimeters; midrib stout, protruding from abaxial surface of lamina, slightly curved; secondaries seven to nine, sub-opposite, leaving midrib at angles of from 60° to 90°, camptodrome, with small branches toward the margins; the basal pair of the secondaries in two of the specimens are straighter, and diverge from the midrib at smaller angles than the secondaries above; tertiaries obscure, apparently irregularly percurrent; margin finely serrate; texture thin.

Discussion—Of the described fossil species of *Prunus* only *P. coloradensis* Knowlton¹ of the Raton flora resembles the present fossils. This species differs from the San Pablo material by having a cuneate base, and a generally different cast to the whole leaf. The living species that most closely resembles the fossils is *P. serotina* Ehrh., which is distributed throughout the southeastern states. *P. japonica* Thunb. of Asia also bears some relation, but always has a long acuminate tip which seems to be lacking in the fossils. Knowlton noted the similarity of the Raton species to *P. serotina*, a fact that suggests the San Pablo material may be the same as the Raton species. The incompleteness of that material and mine makes it advisable to keep the two separate for the present, although more material may show that they are the same. *P. serotina* is widely distributed in eastern North America, from Texas and North Dakota to New Brunswick and Florida, growing in both moist and dry situations, but not actually in the swamps.

Occurrence—Loma Ranch, Locality 607; Bailey Road, Locality 618; Altamont Pass, Locality 199; Corral Hollow, Locality P361.

Collection—Univ. Calif. Mus. Pal., Cotypes, Nos. 1265, 1266; Paratype, No. 1264.

Genus ROSA Linné

Rosa hillia Lesqx.

Rosa hillia Lesquereux, U. S. Geol. Surv. Terr. Rept., vol. 8, p. 199, pl. 40, figs. 16, 17, 1883.

Eleven specimens of this species have been collected from the San Pablo localities. They appear to be identical with Lesquereux's species and with those reported by Chaney from the Crooked River Basin.² The modern *R. woodsii* Lindl. of the middle western prairies has leaves that are closely similar to the fossils, although not more so than *R. nutkana* Presl., which is widely distributed in western America.

Occurrence—Loma Ranch, Locality 607; Bailey Road, Locality 618.

Collection—Univ. Calif. Mus. Pal., Nos. 1267, 1268.

¹ Knowlton, U. S. Geol. Surv. Prof. Paper 101, p. 326, pl. 96, fig. 2, 1917.

² Chaney, R. W., Carnegie Inst. Wash. Pub. No. 346, p. 123, pl. 13, figs. 8-10, pl. 14, fig. 1, 1927.

ORDER SAPINDALES
Family AQUIFOLIACEÆ

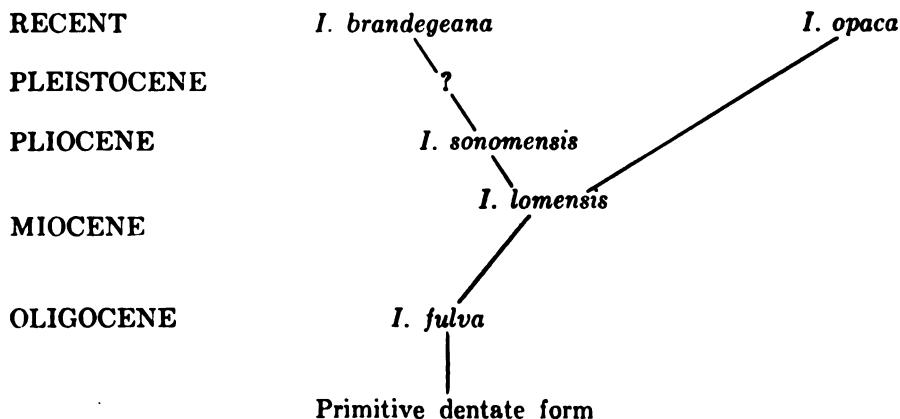
Genus *ILEX* Linné

Ilex lomensis n. sp.

(Plate 7, figs. 3, 4)

Four specimens of this species are present in the San Pablo collections. None of these is complete, yet together they show characters that clearly separate them from any previously described species of this genus.

Description—Leaves lanceolate; tip missing; base truncate; length preserved 9 centimeters, in life probably 12 or more; width 4 to 5 centimeters; petiole missing; midrib prominent, straight; secondaries numerous, leaving the midrib at low angles, curved convexly toward the apex, fourteen showing on the largest fragment, alternate to sub-opposite, with much smaller sub-secondaries springing from the midrib between them, camptodrome, dividing near the margin with one branch running parallel to the margin and about 1 or 2 millimeters inside of it, the other turning downward to meet the next lower secondary's upward branch; tertiaries distinct, reticulate, making fairly large polygons on the lamina; margins thickened, entire, with a few remote, broad, spine-tipped points; texture coriaceous to subcoriaceous.



Discussion—This species is most closely related to the living *Ilex opaca* Ait., and to the fossil *I. sonomensis* Dorf¹ and *I. fulva* MacGinitie.² Of the two fossil species the former is younger and the latter is older. *I. sonomensis* is smaller and shows a tendency toward a more entire form than the San Pablo species, while *I. fulva* is considerably larger and appears to have more numerous teeth as a rule.

The development shown by these three species is significant in connection with the development of the climate in this region during the time represented by the fossils. The oldest form, *Ilex fulva*, is a large and luxuriant leaf, larger indeed than its living equivalents, indicating optimum conditions for growth with ample moisture and warm temperature. *I. lomensis*

¹ Dorf, E., Carnegie Inst. Wash. Pub. No. 412, p. 101, pl. 12, figs. 6, 7, pl. 13, figs. 1, 2, 1933.

² MacGinitie, H. D., Carnegie Inst. Wash. Pub. No. 465, III, p. 145, pl. 10, figs. 1, 2, pl. 12, fig. 1, 1937.

is smaller and probably somewhat thicker, indicating slightly less favorable conditions for growth, while *I. sonomensis* is quite small and thick. This together with the pronounced tendency toward an entire form is an indication of a habitat under unfavorable conditions of moisture and perhaps temperature. These changes in leaf characters are to be correlated rather closely with the changes in climate indicated for this region and time by the interpretation of the fossil floras. The accompanying figure suggests the relationships of these species to each other and to certain living species in this genus.

This chart suggests that these species developed from the preceding ones: whether this is true, or whether they were all in existence at the same time and merely followed each other through the region cannot be determined at this time.

Occurrence—Loma Ranch, Locality 607.

Collection—Univ. Calif. Mus. Pal., Cotypes Nos. 1269, 1270.

ORDER RHAMNALES

Family RHAMNACEÆ

Genus BERCHEMIA Neck.

Berchemia multinervis Heer

Berchemia multinervis Heer. Lesquereux, U. S. Geol. Surv. Terr. Rept., vol. 7, p. 277, pl. 52, figs. 9, 10, 1878.

Seven specimens of this genus are included in the San Pablo collections, all of them obviously the same as the species reported by Lesquereux. The shape, the margin, and the venation are exactly similar. The fossils are matched in every detail by the leaves of *B. scandens* Trelease, which grows today throughout the southeastern states in moist shady situations.

Occurrence—Loma Ranch, Locality 607.

Collection—Univ. Calif. Mus. Pal., No. 1272.

ORDER PARIETALES

Family DILLENIACEÆ

Genus TETRACERA Linné

Tetracera castaneæfolia MacGinitie

Tetracera castaneæfolia MacGinitie, Carnegie Inst. Wash. Pub. No. 465, p. 148, pl. 10, fig. 5, pl. 11, figs. 1, 2, 1937.

Castanea ungeri Heer, U. S. Geol. Surv. Terr. Rept., vol. 8, p. 246, pl. 52, fig. 5, 1883.

Lesquereux reported *Castanea ungeri* from Corral Hollow, one specimen¹ of which was found in his collections at the University of California. This specimen is quite different from the leaf that I collected and referred to *Castanea*. It is broader and longer, with more numerous secondaries, apparently has less pronounced teeth and more numerous, more regularly percurrent tertiaries. In all the preserved characters it is the same as the Weaverville *Tetracera*, and differs from *T. oregona* Chaney and Sanborn² in the same characters that MacGinitie's species does. It is separated from *T. spokaneensis* Brown³ by its straighter secondaries, more numerous teeth,

¹ This specimen is figured on plate 52, fig. 5, U. S. Geol. Surv. Terr. Rept., vol. 8, 1883.

² Chaney, R. W., and Sanborn, E. I., Carnegie Inst. Wash. Pub. No. 439, pp. 87-90, 1933.

³ Brown, R. W., U. S. Geol. Surv. Prof. Paper 186-J, p. 182, pl. 63, figs. 6, 7, 1937.

and more regularly percurrent tertiaries, which are uniformly normal to the secondaries.

On the basis of its present distribution, this genus might be considered incongruous in this flora. Its climatic requirements are somewhat different from the remainder of the San Pablo species. However, it has been found in association with many of them in two older and more northern fossil floras, both of which are temperate or warm temperate, as well as in a typically subtropical one, where it is to be expected. It may be considered here as a relict of a formerly widespread subtropical forest, barely maintaining itself against imminent extinction. Its scarcity in the collections suggests that it was rare in the Neroly forests, and it is so far unrecorded from Pliocene floras of western America, nor is its occurrence to be expected in them, unless it be in those much farther south. *Tetracera castaneæfolia* has been referred to *T. volubilis* Linné, a vine or scandent shrub in damp forests from southern Mexico to Brazil and in the West Indies.¹

Occurrence—Corral Hollow, locality unknown.

Collection—Univ. Calif. Mus. Pal., Plesiotype, No. 1287.

ORDER MYRTALES

Family MYRTACEÆ

Genus MYRTUS (Tourn.) Linné

Myrtus oregonensis Lesqx.

Myrtus oregonensis Lesquereux, U. S. Geol. Surv. Terr. Rept., vol. 8, p. 254, pl. 58, fig. 10, 1883.

Lesquereux's type specimen of this species is present in the collections at the University of California, where I have had an opportunity to study it. As Lesquereux said, it closely resembles *M. communis* L. of western Asia. It bears little resemblance to any Nearctic species of myrtaceous plants, although several species of *Myrtus* and *Eugenia*, a related genus, now in Mexico are slightly similar. The fossil may be ancestral to these, or it may be a rare member of the Asiatic element of older floras of western America.

Occurrence—Corral Hollow, locality unknown.

Collection—Univ. Calif. Mus. Pal., Holotype, No. 1288.

ORDER UMBELLALES

Family CORNACEÆ

Genus NYSSA Gronov.

Nyssa knowltoni Berry

(Plate 5, fig. 2)

Nyssa knowltoni Berry, U. S. Geol. Surv. Prof. Paper 154-H, p. 261, pl. 59, fig. 7, 1929.

This species is represented in the San Pablo collections by fragments of leaves and numerous impressions of seeds. The leaves are identical with the Latah material, and the seeds closely resemble those described by Berry from the Citronelle formation of Pliocene age.² I believe that the

¹ MacGinitie, H. D., *op. cit.*, 1937.

² Berry, E. W., U. S. Geol. Surv. Prof. Paper 98-L, p. 203, pl. 47, fig. 8, 1916.

Latah material, the San Pablo material, and the Citronelle material may all represent one species, but in view of the great distance that separates the eastern fossils from the western ones I hesitate to place them together. The San Pablo fossils are unquestionably the same as the Latah species. *N. knowltoni* is most closely matched by *N. aquatica* L. of the southeastern states. Berry does not refer the Latah material to any living species, but from his published figure and the description the reference appears satisfactory. He definitely refers the Citronelle material to *N. aquatica*. *Nyssa knowltoni* has been reported by MacGinitie from the Weaverville beds;¹ he also refers it to *N. aquatica*. This modern species inhabits deep swamps and moist ground in association with *Taxodium distichum*.

Occurrence—Loma Ranch, Locality 607; Altamont Pass, Locality 199.

Collection—Univ. Calif. Mus. Pal., Plesiotype, No. 1275; Nos. 1273, 1274, 1276.

ORDER OLEALES

Family OLEACEÆ

Genus CHIONANTHUS Linné

Chionanthus membranaceus Knowlton

Chionanthus membranaceus Knowlton, U. S. Geol. Surv. Prof. Paper 101, p. 345, pl. 108, fig. 2, 1917.

Only the bases of three leaves of this species have as yet been collected from the San Pablo localities. In all preserved characters they are indistinguishable from the species described by Knowlton from the Raton flora. He pointed out the similarity of the fossil leaves to the leaves of the living *C. virginicus* L. The San Pablo leaves also agree closely with this living species. *C. virginicus* grows most commonly away from the immediate coastal swamps, preferring the rich moist bottomlands along streams at middle and lower elevations. The rarity of *C. membranaceus* in the San Pablo collections indicates that it did not grow at the same sites of deposition, but like its living descendant, occupied areas at some distance from them.

Occurrence—Loma Ranch, Locality 607; Altamont Pass, Locality 199.

Collection—Univ. Calif. Mus. Pal., Nos. 1283, 1284.

INCERTÆ SEDIS

Fruit (?)

(Plate 3, fig. 3)

A cast of what may be the capsule of some plant belonging to the Papaveraceæ has been recovered from the San Pablo beds. It consists of an apparently woody stem about 2 millimeters wide and 1.5 centimeters long, from which rises a conical body 2 centimeters long and about 7 millimeters in diameter in the widest part. The greatest diameter occurs about two-thirds of the way up the length, and is constant from there on. Eleven vertical ribs show upon the surface. The interior is filled with matrix, which is medium coarse sand, somewhat friable, and the plant tissue is represented by a thin brown layer only. The ribs were apparently woody, and are represented by strings of woody material thicker than the rest of the plant remains. A faint suggestion of some sort of cap is present at the upper

¹ MacGinitie, H. D., Carnegie Inst. Wash. Pub. No. 465, III, p. 150, 1937.

end, but is discernible for only a small part of the circumference. This body closely resembles the capsules of *Papaver californicum* Grey now growing in California, and even more closely *P. dubium* L., now present in the eastern coastal states, naturalized from Europe.

Occurrence—Bailey Road, Locality 618.

Collection—Univ. Calif. Mus. Pal., No. 1277.



FIG. 1—Loma Ranch, Locality 607. Looking north.
The section was measured up this hill.



FIG. 2—Corral Hollow, near Locality P361. Looking north. *Quercus lobata* on the valley floor, with chaparral on the slopes. The Neroly is exposed in the cliffs on the nearest slopes and on the hill in the distance.



FIG. 1—Altamont Pass, Locality 199. Looking east. Leaves occur in the bank close to the right-hand edge of the picture.



FIG. 2—Bailey Road, Locality 618. Looking north. Leaves occur in the fine-grained layer near the middle of the outcrop, at the left side of the picture.

PLATE 3

FIGS. 1, 2, 4a—*Taxodium dubium* Heer. Loc. 607. Plesiotypes. Univ. Calif. Mus. Pal., Nos. 1137, 1138, 1285.

FIG. 3—Unidentified fruit. Loc. 618. Univ. Calif. Mus. Pal., No. 1277.

FIGS. 4b, 5 *Smilax diforma* new species. Loc. 607. Cotypes. Univ. Calif. Mus. Pal., Nos. 1144, 1145.



a →



b

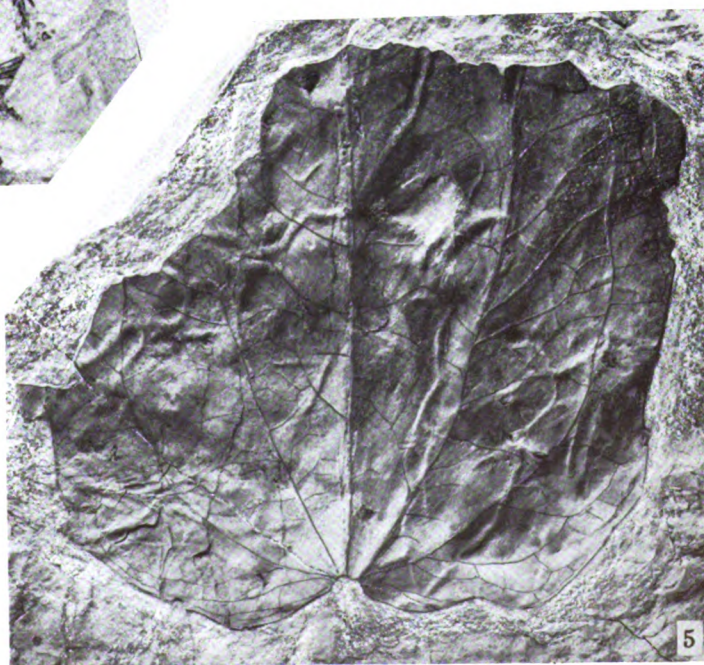


PLATE 4

FIG. 1—*Populus emersoni* new species. Loc. 199. Cotype. Univ. Calif. Mus. Pal. No. 1239.

FIG. 2—*Populus emersoni* new species. Loc. 618. Cotype. Univ. Calif. Mus. Pal. No. 1238.

FIG. 3—*Populus balsamoides* Lesquereux. Loc. 618. Plesiotype. Univ. Calif. Mus. Pal. No. 1236.

FIG. 4—*Myrica diforme* Chaney. Loc. 618. Plesiotype. Univ. Calif. Mus. Pal. No. 1242.

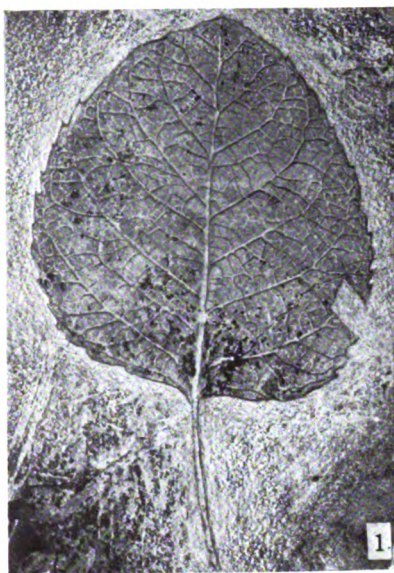


PLATE 5

FIG. 1—*Populus balsamoides* Lesquereux. Loc. 618. Univ. Calif. Mus. Pal., No. 1271.

FIG. 2—*Nyssa knowltoni* Berry. Loc. 607. Plesiotype. Univ. Calif. Mus. Pal., No. 1275.

FIG. 3—*Populus balsamoides* Lesquereux. Loc. 618. Plesiotype. Univ. Calif. Mus. Pal., No. 1237.

FIG. 4—*Prunus chaneyi* new species. Loc. 618. Cotype. Univ. Calif. Mus. Pal., No. 1266.

FIG. 5—*Prunus chaneyi* new species. Loc. 199. Cotype. Univ. Calif. Mus. Pal., No. 1265.



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PLATE 6

FIG. 1.—Birch catkin from the Missoula beds.

FIGS. 2, 3.—*Betula multinervis* Jennings. Loc. 199. Plesiotypes. Univ. Calif. Mus. Pal., Nos. 1248, 1249.

FIGS. 4, 5.—*Alnus corrallina* Lesquereux. From Lesquereux's locality in Corral Hollow. Univ. Calif. Mus. Pal., Nos. 1244, 1246.



PLATE 7

FIGS. 1, 2—*Persea princeps* Schimper. Loc. P361. Plesiotypes. Univ. Calif. Mus. Pal., Nos. 1255, 1256.

FIGS. 3, 4—*Ilex lomensis* new species. Loc. 607. Cotypes. Univ. Calif. Mus. Pal., Nos. 1269, 1270.



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